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Reprinted from JOURNAL OF BACTERIOLOGY
Vol. 60, No. 6, December, 1950

SOME EFFECTS OF HYDROSTATIC PRESSURE ON THE MULTIPLICATION AND MORPHOLOGY OF MARINE BACTERIA[1]

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Received for publication September 5, 1950

Hydrostatic pressure in the sea, which increases approximately 0.1 atmosphere per meter of depth, appears to be a factor that influences bacterial activities. This was indicated by the observations of Certes (1884*a*,*b*), Certes and Cochin (1884), and Regnard (1884*a*,*b*). The reports of Chlopin and Tammann (1903), Hite *et al.* (1914), Larson *et al.* (1918), and more recent ones reviewed by Macheboeuf *et al.* (1933), Cattell (1936), and Basset *et al.* (1938) indicate that the critical pressure tolerance of microorganisms ranges from 3,000 to 12,000 atmospheres, which is higher than pressures characteristic of the greatest known depth of the sea, the latter being of the order of 1,100 atmospheres. The apparent discrepancies are probably due to differences in experimental conditions, including growth phase, species, culture medium, temperature, time, and other factors now known to influence the pressure tolerance of microorganisms.

ZoBell and Johnson (1949) found that many common microorganisms from surface soil and shallow water were killed in the logarithmic phase of growth in 48 hours at 30 C by pressures of only 500 to 600 atmospheres, and multiplication of some microorganisms was inhibited at 300 atmospheres. Resting cells, endospores, and bacteria from the deep sea were found to be more pressure-tolerant as were organisms pressurized at higher temperatures. The term "barophilic" was coined to describe organisms that grow preferentially or exclusively at high hydrostatic pressures. Such bacteria have been found in the deep sea and also in brines from deep oil wells. Their counterparts that grow only at relatively low pressures, say up to 200 atmospheres, are described as "barophobic." Those that tolerate high pressures but grow best at normal pressures are described as "baroduric." The present paper is concerned primarily with observations on the occurrence and behavior of barophilic, barophobic, and baroduric bacteria in the sea.

METHODS

Bacterial cultures in the logarithmic phase of growth were transplanted to nutrient broth in small test tubes, size 10 × 50 mm, each having a sand-blasted area for numbering with a pencil. The nutrient broth used for this purpose consisted of 0.5 per cent peptone, 0.5 per cent yeast extract, and 0.01 per cent ferric phosphate in aged sea water (ZoBell, 1946). Following autoclave sterilization its reaction was pH 7.5. The medium was inoculated with enough cells to give from 100 to 1,000 per ml. The tubes were stoppered with no. 000 neoprene stoppers that, under the influence of external pressure, functioned as piston thereby subjecting the contents of the tubes to virtually the same pressure a that of the external hydraulic fluid. Enough air was entrapped in each tube t provide for aerobic growth.

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[1] Contribution from the Scripps Institution of Oceanography, New Series 491. This paper is a contribution from the American Petroleum Institute Research Project 43A.

From 20 to 24 culture tubes were placed in each pressure vessel, after whic the latter was filled with water treated with Lugol's iodine to give 5 ppm o free iodine. That no iodine enters the culture tubes has been established b chemical tests, and numerous runs without iodine prove that it has no effec on the activity of cultures in the stoppered tubes. Repeated tests have demonstrated that the cultures never become contaminated by being pressurized eve when the water in the pressure vessel has a rich microflora. The iodine treatment is to minimize contamination when the tubes are opened after bein removed from the pressure vessel.

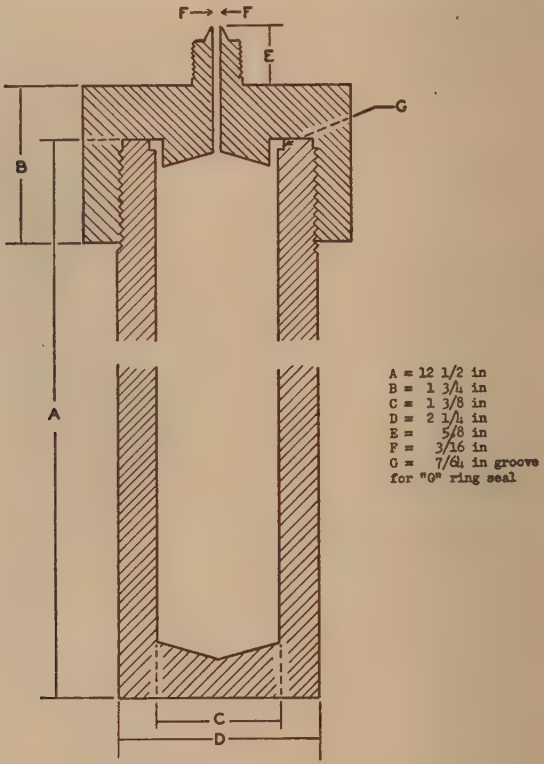

Figure 1. Cross-section of vessel for maintaining microorganisms at high hydrostati pressures.

Pressure vessels (figure 1) consist of 18-8 stainless type 303 steel cylinder 12 inches long, having an outside diameter of $2\frac{1}{4}$ inches and an inside diamete of $1\frac{3}{8}$ inches and fitted with an "O" ring seal held in place by a steel cap 3 inche in diameter. The groove for the "O" ring seal must be machined to be slightly smaller than the "O" ring. With a groove $\frac{7}{64}$ of an inch deep we used "O" ring seals type AN6227B-24, having a width of $\frac{1}{8}$ of an inch, an inside diameter of $1\frac{5}{16}$ inches, and an outside diameter of $1\frac{9}{16}$ inches, obtained from the Parker Appliance Company, Cleveland, Ohio.

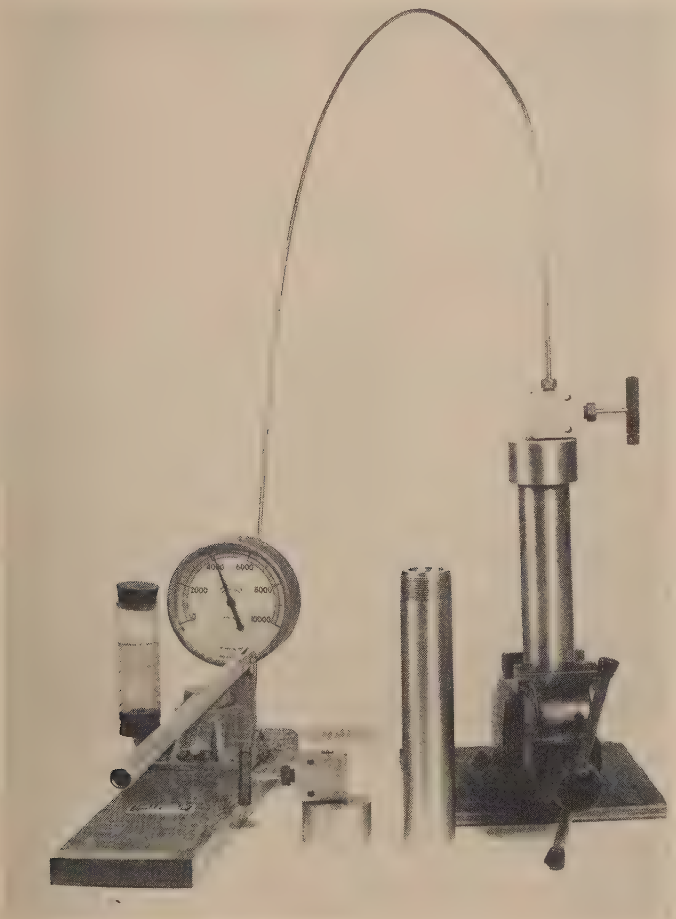

Figure 2. Assembled pressure vessel connected with hydraulic pump.

The steel cap is machined on top to take an Aminco superpressure needle valve, which provides for connecting with the hydraulic pump by means of a length of semiflexible stainless steel superpressure tubing (figure 2). A mixture of 50:50 glycerol and water has proved to be a satisfactory hydraulic fluid for use in the pump and connecting lines. After the vessels have been pressurized, the needle valve is closed, pressure on the line is released, and the tubing is disconnected, the latter being the only operation that requires the use of a wrench. Then the pressure vessels are incubated while submerged in thermostatically controlled water baths.

The pressure vessels filled with water and cultures must be brought to equilibrium with the temperature at which they are to be incubated before pressur is applied. Otherwise changes in temperature may cause changes in pressure. At the termination of each experiment, the pressure vessels are reconnecte with the hydraulic pump and gage in order to check the terminal pressure. We have never experienced a failure from the loss of pressure in any of ou three dozen vessels because, if this apparatus holds the pressure initially, i seems to hold it quite indefinitely. These vessels have been designed to tolerat pressures up to 3,000 atmospheres at 100 C, and all have been tested at 2,00 atmospheres. An atmosphere is equivalent to 760 mm Hg, 14.696 psi (pound per square inch), 1.013 × 10^6 dynes per cm^2, 1.0332 kg per cm^2, or 1.0133 bar, al of these units being used in the literature on hydrostatic pressure.

RESULTS

With relative turbidity as a criterion of multiplication in nutrient sea wate broth, it has been found that, whereas some few cultures of marine bacteri multiplied just as rapidly at 600 atmospheres as at one atmosphere, the multiplication of most cultures was inhibited by pressures ranging from 200 to 60 atmospheres at 30 C (table 1). Out of a total of 56 new species of marine bacteri described by ZoBell and Upham (1944) tested in duplicate, the multiplicatio of 20 was retarded at 200 atmospheres, 35 were adversely affected by a pressur of 400 atmospheres, and 48 were inhibited at 600 atmospheres. Five of the 5 cultures were dead (designated "d" in table 1) after 96 hours at 200 atmospheres as indicated by their loss of ability to multiply in nutrient broth at atmospheri pressure. Twelve of the 56 were killed by 400 atmospheres and 33 were killed b 600 atmospheres in 96 hours at 30 C.

Contrary to the generalization of Certes (1884*a*) that marine microorganism are more resistant to high pressure than fresh-water forms, these results indicat that marine bacteria are just as susceptible to pressure effects as fresh-wate species (ZoBell and Johnson, 1949). Whether our results were influenced b the fact that the pure cultures had been maintained in the laboratory at atmospheric pressure for several years is problematical.

Observations on recent isolates and mixed cultures, which have not bee identified as to species, indicate that marine bacteria indigenous to shallo depths are affected by hydrostatic pressure in much the same way as freshwater forms from surface materials. However, certain cultures collected a depths of several thousand feet from the sea floor or from oil well brines (ZoBell 1950) have been found to grow readily at pressures isobaric with the environmen from which they were taken. A few cultures, including a *Desulfovibrio* species have proved to be obligate barophiles, which grow only at high pressures. Th identification of such organisms presents special problems because standar methods for the study of pure cultures are all based upon the behavior an appearance of bacteria at atmospheric pressure. Moreover, evidence is accumulating that, besides affecting the viability and multiplication of bacteria, pressure also has pronounced effects on their metabolism and morphology. The salinity and other properties of the medium in which bacteria are maintained also affect their susceptibility to pressure.

Certain microorganisms that tolerate elevated pressures do so with attendant changes in morphology. This may be illustrated by the results with *Serratia marinorubra*. When cultivated in nutrient sea water broth at ordinary pressures, this organism appears as a small rod, 0.3 to 0.5 microns wide by 0.6 to 1.5 microns long, occurring singly or in pairs (figure 3 *A*). When cultivated in similar medium at a pressure of 600 atmospheres, *S. marinorubra* grows in filaments up to 200 microns in length with no evidence of fission (figure 3 *D*). When allowed to stand for a few minutes at atmospheric pressure, these filaments start to fragment into short cells identical with the original culture, a process requiring only an hour or two for completion at 25 C. In fact, one can watch the fission of the long filaments in moist preparations on the field of a phase microscope. Techniques are now being perfected for fixing the cells before they are depressurized, since it has not yet proved to be feasible to examine them microscopically at high pressure.

TABLE 1

Multiplication as indicated by turbidity (− or + to ++++) or death of marine bacteria in nutrient broth after 96 hours' incubation at 30 C at different hydrostatic pressures

NAME OF ORGANISM*	HYDROSTATIC PRESSURE IN ATMOSPHERES			
	One	200	400	600
Achromobacter stationis	++++	++++	++++	−
Achromobacter thalassius	++++	−d	−d	−d
Actinomyces marinolimosus	++++	++++	−	−
Actinomyces halotrichis	++++	−	−	−
Bacillus epiphytus	++++	+++	++	−d
Bacillus borborokoites	++++	++++	++++	+++
Flavobacterium neptunium	++++	+	−	−
Micrococcus euryhalis	++++	−d	−d	−d
Micrococcus sedentarius	++++	++++	++++	−d
Micrococcus aquivivus	++++	++++	++++	++++
Pseudomonas obscura	++++	++++	−	−d
Pseudomonas hypothermis	++++	−d	−d	−d
Pseudomonas perfectomarinus	++++	++++	++++	++++
Serratia marinorubra	++++	++++	++	−
Vibrio algosus	++++	++++	+++	++
Vibrio marinoflavus	++++	−	−d	−d
Vibrio ponticus	++++	+++	++	−d

* These are new species of marine bacteria described by ZoBell and Upham (1944).

S. marinorubra and *Vibrio phytoplanktis* lost their motility and all evidence of flagellation when incubated in nutrient broth for a few hours at 400 to 600

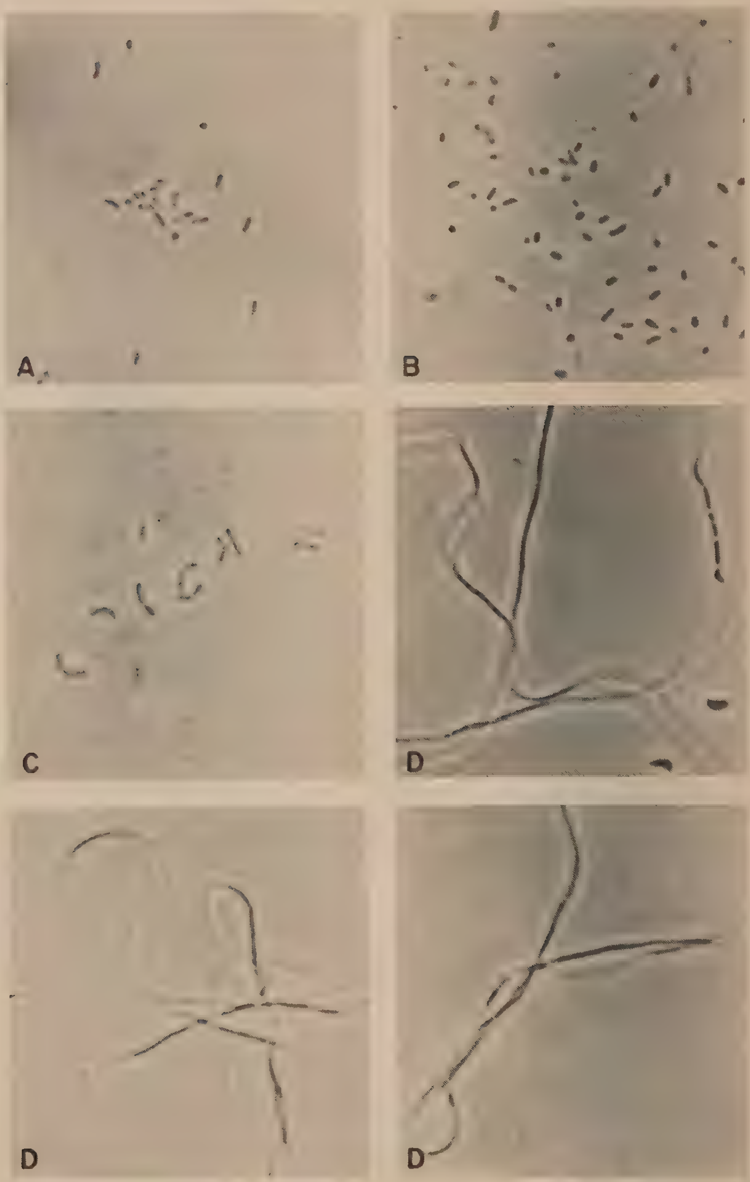

Figure 3. Photomicrographs of *Serratia marinorubra*, in wet preparation by Spence phase contrast microscope with 97 × dark M objective, shortly after removal from pressure vessels in which cells had incubated for 4 days in nutrient broth at 23 C; A at 1 atmosphere, B at 200 atmospheres, C at 400 atmospheres, and D at 600 atmospheres (× 1,000)

atmospheres. These properties as well as normal morphological appearance were restored when the pressurized cultures were incubated at room pressure and temperature for a few hours. Most of the bacteria studied by Chlopin and Tammann (1903) allegedly lost their motility at around 3,000 atmospheres. The motility of *Amoeba dubia* and *Amoeba proteus* was stopped by pressures of 250 atmospheres, according to Marsland and Brown (1936). Ebbecke (1935) noted a loss of motility in paramecia when they were compressed to 600 atmospheres, the effects of pressure being immediately and completely reversible if pressure was released within a short time.

Neither the morphology nor the motility nor the viability of bacterial cells seems to be affected immediately by pressure, thereby suggesting that compression exerts itself not directly through physical force in the sense of something's being crushed but rather indirectly by affecting the physicochemical equilibria of the system. Both time and temperature influence the results. The examination of cells of *S. marinorubra* in wet preparations by phase contrast microscope immediately after they were removed from the pressure vessels revealed that in nutrient broth they appeared normal in size and motility for 6 to 8 hours at a pressure of 400 atmospheres, but after 16 hours they had lost their motility, and long filaments started to appear. Three other barophilic rods, 46:178 and 46:188 not yet identified as to species and *Flavobacterium okeanokoites*, have likewise been observed to develop into long unfragmented filaments when cultivated at 600 atmospheres. Cells of *Bacillus borborokoites*, *Bacillus abysseus*, *Vibrio phytoplanktis*, and an unidentified rod 46:125 were abnormally elongated when cultivated at 400 to 600 atmospheres, but not nearly to the same extent as *S. marinorubra*. Cells of *Micrococcus aquivivus* and *Sarcina pelagia* were larger in size and more bunched when cultivated at elevated pressures. On the other hand, the morphology of *Vibrio haloplanktis* and *Achromobacter stationis* was not perceptibly influenced by pressures of 400 atmospheres. How general the effect of pressure is on the fission and morphology of barophilic bacteria can be ascertained only by further observations. The cleavage of eggs of the sea urchin was found by Marsland (1938) to be repressed by pressures exceeding 333 atmospheres or even reversed at certain stages when a pressure of 450 atmospheres was applied. Draper and Edwards (1932) observed that subjecting *Fundulus* eggs for from 30 minutes to 3 hours to pressures ranging roughly from 90 to 130 atmospheres retarded the rate of cell division.

Plate counts (table 2) substantiate direct microscopic observations that, although *S. marinorubra* grows in size (length) at 400 to 600 atmospheres, it does not multiply (increase in number of cells) appreciably. Nutrient broth was inoculated with approximately 10,000 viable cells per ml. After 2 days' incubation there was a diminution in the number of viable cells of some of the cultures incubated at elevated pressures, the lethal or inhibitory effect of pressure being more pronounced at 10 C than at 25 C. ZoBell and Johnson (1949) also observed that, within the critical range of bacteria, lower temperatures markedly accentuated the growth-retarding and disinfecting effects of pressure. This generalization, however, does not apply to all microbial reaction as will be elaborated in subsequent communications.

A study of growth curve data (figure 4) shows that the multiplication *S. marinorubra* in nutrient broth was retarded by a pressure of only 50 atmo

TABLE 2

Number of viable cells, as indicated by plate counts, after 2 days' incubation at different temperatures and pressures in nutrient broth inoculated with approximately 10,000 cells per ml

CULTURE	TEMPERATURE	HYDROSTATIC PRESSURE IN ATMOSPHERES			
		One	200	400	600
Serratia marinorubra	10 C	2,000,000	5,000	5,000	3,000
	25 C	40,000,000	40,000,000	10,000,000	1,000,000
Micrococcus aquivivus	10 C	20,000,000	2,000	1,000	30
	25 C	30,000,000	20,000,000	3,000,000	1,000
Pseudomonas obscura	10 C	10,000,000	200	90	0
	25 C	300,000	200,000	8,000	0
Pseudomonas hypothermis	10 C	40,000	500	60	0
	25 C	6,000,000	2,000,000	500,000	0

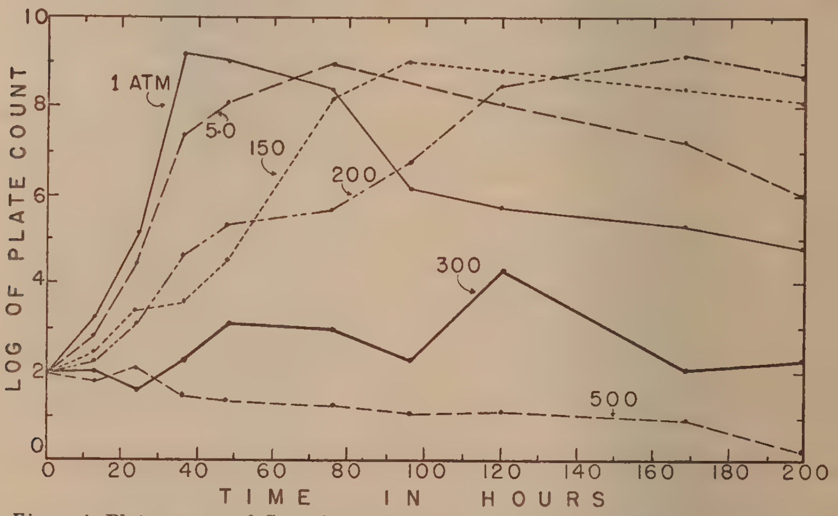

Figure 4. Plate counts of *Serratia marinorubra* after different periods of incubation in nutrient broth at 23 C at pressures ranging from 1 to 500 atmospheres.

pheres, although the total number of viable cells, as indicated by plate count procedures, eventually reached almost the same level at 50 to 200 atmospheres as at atmospheric pressure. At 300 atmospheres there was virtually no multiplication, and at 500 atmospheres there was actually a decrease in the numbe of viable cells as indicated by plate counts. This was confirmed by the direct microscopic observation of pressurized cultures, the cells of which increased in ength, but not in number, at 500 atmospheres.

DISCUSSION

Accumulating data suggest that most barophobic bacteria in the logarithmic phase of growth are killed by prolonged exposure to hydrostatic pressures ranging from 200 to 600 atmospheres at temperatures ordinarily optimum for their multiplication. The mechanism of the growth-retarding and disinfecting action of such pressures is still obscure although believed by the authors to be associated with vital chemical reaction rates that are irreversibly retarded at critical pressures and temperatures. Studies now in progress show that nitrate reduction, starch hydrolysis, gelatin liquefaction, and other bacterial reactions easily observed at elevated pressures are differentially affected. The studies of Johnson (1947) and his co-workers (1946, 1948) on the rational interpretation of biological reaction rates indicate that hydrostatic pressure exerts itself through its effect on volume changes. Significantly Johnson and Eyring (1948) point out that the mechanism responsible for the effect of pressure of the order of 500 atmospheres is probably quite different from the effect of pressure of the order of 10,000 atmospheres, which has been known for several years to denature proteins, kill microorganisms, inactivate enzymes, alter antibodies, etc., at room temperature (Cattell, 1936; Bridgman, 1946).

Indications are that hydrostatic pressure, within the range occurring in the deep sea, is a thermodynamic factor of co-ordinate importance with temperature in affecting the distribution and physiological activities of microorganisms. Besides the promise of yielding information fundamental to a fuller understanding of life processes by adding pressure to temperature as a variable in the equation of state, further studies on hydrostatic pressure are needed to explain certain conditions in the sea.

All workers in the past (see review by ZoBell, 1946) have attempted to appraise the importance of bacteria in the sea upon a basis of bacterial behavior at atmospheric pressure. Although certainly some bacteria from the deep sea will multiply at atmospheric pressure, such organisms may be transients settled recently from surface water while the indigenous flora may have been missed by plate counts or other cultural procedures. Also we have cause to wonder whether, under the influence of prevailing pressure in the deep sea, bacteria *in situ* show the bizarre morphology exhibited by *Serratia marinorubra* and other barophilic varieties observed under laboratory conditions. To what extent may the rate of nitrification, nitrate reduction, nitrogen fixation, cellulose digestion, and other reactions catalyzed by bacterial enzymes be influenced by pressure in the deep sea? Such questions may be answered only by further observations.

The observations reported in this paper are concerned primarily with the behavior of bacteria at pressures ranging from 200 to 600 atmospheres, the lower part of which range appears to be critical for the activity of most bacteria at room temperature. However, as will be detailed in subsequent reports, we have observed barophilic bacteria in the logarithmic phase of growth which tolerate pressures approximating the highest found in the sea. Certain *D* *sulfovibrio* species, for example, isolated from great depths, reproduced an reduced sulfate more rapidly at 1,000 atmospheres than at lower pressure Although most of the bacteria in marine mud samples were sterilized by 1,60 atmospheres at 40 C in 4 days, two *Micrococcus* species and one *Bacill* species survived these conditions.

The ability of bacteria to become acclimatized to various pressures has r ceived attention without conclusive results to date, although we have obtaine some evidence that hydrostatic pressure induces genetic changes. Accordin to McElroy and de la Haba (1949), pressures of the order of 150 to 600 atmo pheres increased the number of biochemical mutants in cultures of *Neurospor crassa* treated with nitrogen mustard but depressed the number of morphologic mutants obtained from such cultures in direct proportion to the pressure ap plied.

The rate of pressurizing and decompressing bacterial cultures is inconsequen tial except when dealing with compressed gases. Though related, the proble of the effects of compressed gases on microorganisms differs in many respect from that of the effects of hydrostatic pressure.

ACKNOWLEDGMENT

The authors are pleased to acknowledge their indebtedness to Nance Fountain Rose Marie Cassady, and Jean S. ZoBell for technical assistance. The con structive criticisms of Dr. Frank H. Johnson are also acknowledged. The wor was supported in part by a grant from the American Petroleum Institute an grant no. 1250 from the University of California Committee on Research.

SUMMARY

Apparatus and techniques are described for studying the effect of hydro static pressures up to 2,000 atmospheres or roughly 30,000 psi (pounds pe square inch) on the multiplication and viability of bacteria.

The multiplication of most marine bacteria was retarded by pressures ranging from 200 to 600 atmospheres, and a good many were killed in 2 to 4 day at 30 C by such pressures although some barophilic varieties from great depth grew at higher pressures.

Confirming previous reports, pressure effects were found to be influenced by the temperature, bacteria in general tolerating higher pressures at higher temperatures.

Elongated cells and other bizarre morphological forms of certain barophilic bacteria developed in nutrient broth at high hydrostatic pressures. *Serratia marinorubra* grew in size with no evidence of multiplication or fission at 400 to 600 atmospheres. Motility was lost.

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Ictalurus lambda, a New Catfish, Based on a Pectoral Spine from the Lower Pliocene of Kansas

By Carl L. Hubbs and Claude W. Hibbard

Reprinted from Copeia, 1951, No. 1, March 21

Ictalurus lambda, a New Catfish, Based on a Pectoral Spin from the Lower Pliocene of Kansas[1]

By Carl L. Hubbs and Claude W. Hibbard

THE pectoral spine herein described as *Ictalurus lambda* is referred to th family Ameiuridae, of the siluroid (nematognathous) division of th Ostariophysi, not only because it agrees most satisfactorily with the pectora spines at hand of Recent species of that family, but also because of varie circumstantial evidence. This family comprises the North American fresh water catfishes and is thought to date, at least, from the Eocene. It is plausible inference that this group lived in the streams that laid down th Ogallala formation in a climate that appears to have been mild-temperate.

It is highly improbable that the spine should be referred to the rathe similar South American family Pimelodidae. That group now ranges northward only to southern Mexico and probably did not occur much farther nort in the Pliocene. In fact, Middle America appears to have been invaded onl recently by the pimelodids, for the many Middle American species are al referred to *Rhamdia*, which is only one of the numerous South America genera. Similarly, Middle America seems to have been invaded by only on genus of the Cichlidae, namely *Cichlasoma*, which has subsequently undergone only specific and weak generic differentiation. Other South America derivatives have passed through little evolutionary change in Middle America A plausible assumption is that the northward dispersal followed the closur of the Panama Portal, probably in Pliocene time. There are no reasons t suspect the pertinence of the fossil to any other Neotropical family of th Nematognathi (Siluroidea) or to any Old-World family.

Reference of the spine to the Ariidae (the marine catfishes) also appear improbable, for it is only within the tropics that a few representatives of tha family have become established in fresh water. It is not to be expected tha an ariid would have penetrated to the northward and into the interior as fa as Kansas during the mild-temperate Pliocene.

Certain differences in structure, outlined below, confirm the separation o the fossil from *Rhamdia* and from the Ariidae.

The spine is tentatively placed in the genus *Ictalurus* because of its larg size, because of certain points of agreement in structure, and because it i plausible to assume that this primitive genus of the Ameiuridae occurred i the Kansas region during the Lower Pliocene.

Terminology of Pectoral Spine

In order to describe this pectoral spine completely and understandabl and to compare it with the spines of Recent species, it is necessary to propos terms for the complex processes and recesses of the locking mechanism. Th terminology of previous workers has been found inadequate. Thilo (1896) used descriptive German terms. Sőrensen (1898) assigned Greek letters to the processes and used a few descriptive English terms. Merriman (1940) used numbers, correlating them with the Greek letters of Sőrensen.

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[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 492, and from th Department of Geology of the University of Michigan.

The structures are readily homologized throughout the Ameiuridae, Pimelodidae and Ariidae, as these families are represented by pectoral spines in the University of Michigan Museum of Zoology. The terms anterior and posterior are applied to the spine as it is seen when locked at right angles to the body.

The *shaft* (Pl. II, Fig. 1) of the pectoral spine is flattened dorsoventrally. The *anterior edge* (Pl. I, Fig. 3), called "the foremost denticulated edge of the ray" and "R" by Sőrensen, is usually ridged and often bears *anterior dentations* (Pl. III, Fig. 1). The *posterior edge* (Pl. II, Fig. 2) is more often or more strongly dentate (Pl. I, Fig. 4). The dentations may be *antrorse* when directed more or less distad, *retrorse* when directed proximad, or *erect*. Proximally, where reduced in size, the *posterior dentations* may arise from a *posterior groove* (Pl. III, Fig. 2), which extends toward the distal end of the basal recess, described below. Distally, just beyond the last of the posterior dentations, there is a bony point, the *end of the ossification* (Pl. 2, Fig. 1), where spinous structure abruptly gives way to the soft, segmented, and often more or less filamentous tip of the first ray. The *basal recess* (Pl. II, Fig. 2) is a deep cavern on the posterior face of the base of the shaft of the spine. Its outer rim is rather indistinct. At its distal end, the cavity of the recess is continuous, openly or through a pore, with the hollow center of the spine. The proximal face of the basal recess is largely occupied by a more or less elevated articulating *basal process* (Pl. III, Fig. 2). Adjacent to this process, across the proximal face of the base of the spine, is a more or less oval *central articulating surface* (Pl. II, Fig. 2), which usually has two more or less distinct surfaces, of which the *ventral facet* (Pl. I, Fig. 1) is smaller than the *dorsal facet* (Pl. I, Fig. 1). The rims of the central articulating surface are more or less elevated. In some species, in which it is especially elevated, the posterior rim may be known as the *posterior process* (Pl. I, Fig. 4). It is generally much less conspicuous than the three major processes—dorsal, anterior, and ventral.

The dorsal process (Pl. III, Fig. 1) is much the largest. It was called "δ" by Sőrensen, "arched crest" by Burkenroad (1931), and "2" or "an arched crest of base" by Merriman. This process arises abruptly from the flattened dorsal surface of the base of the spine. Its proximal face is very broad and more or less concave. The outer edge is variably arched (convex outward) and is either rounded or flattened. On the proximal face of the process, close to the dorsal end of the central articulating surface, and just ventral to the edge of the finely sculptured *dorsal articulating surface* (Pl. I, Fig. 1), the *proximal tubercle* (Pl. II, Fig. 2) is more or less evident. It may be obsolescent, somewhat compound, or modified into a ridge. Toward the base of the posteroproximal edge of the dorsal process, and outside the posterior process, is a shallow to deep, straight or angulated, more or less lanceolate *posterior fossa* (Pl. III, Fig. 2). At the opposite, anterior part of the base of the spine, between the dorsal and anterior processes, is a more or less definite *anterior fossa* (Pl. II, Fig. 1), pointed at the distal end and open proximally. The fossa may be continued as a shallow groove on the anterodorsal face of the anterior process. Opposite the open end of the fossa is a strong strut, of varying shape, connecting the dorsal and anterior processes. This structure will be referred to as the *proximal crest* (Pl. II Fig. 1).

The *anterior process* (Pl. II, Fig. 3), the most proximal projection, is a more or less capitate structure with a roughened *proximal articulating surface* (Pl. II, Fig. 3). The shape of the process and the orientation of the articulating surface are often distinctive. The anterior process is the "β" of Sőrensen the "1" of Merriman. The anterior process is separated from the ventral process by a deep U- or V-shaped *anteroventral emargination* (Pl. II, Fig. 1)

The *ventral process* (Pl. II, Fig. 1) arises at the proximal end of a basal ridge on the ventral face of the spine. Its base is more flattened than the base of either the dorsal or the anterior process. It varies much in shape but is usually bicapitate, with a *proximal lobe* (Pl. II, Fig. 3) and a *distal lobe* (Pl. II, Fig. 2), between which a *ventral fossa* (Pl. II, Fig. 3) may be developed. In addition, in some species, there is a *ventral rim of ventral process* (Pl. II, Fig. 2), on the ventral edge of the distal lobe, and a *dorsal rim of ventral process* (Pl. II, Fig. 2) on the dorsal edge of the proximal lobe.

AGE VARIATION IN THE PECTORAL SPINE

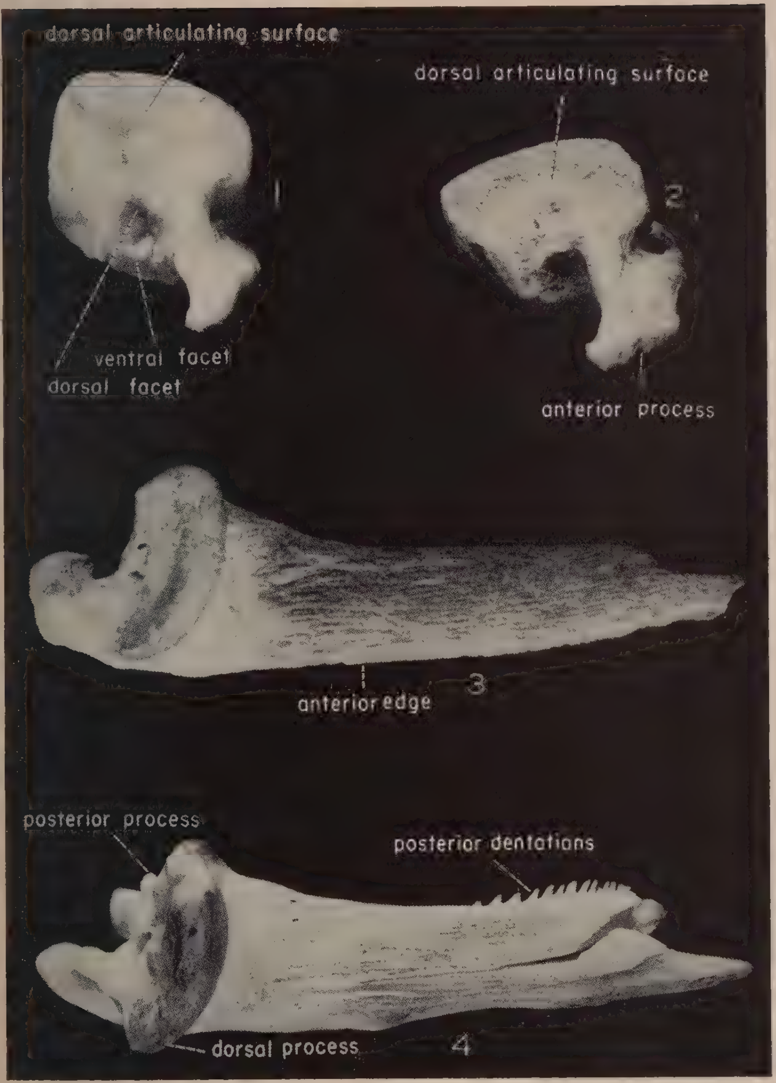
With the increasing age of the fish, the spine changes enormously in structure. It becomes much heavier and relatively shorter and the tip often becomes broken. In many species the surface becomes striated and rugose The dentations increase in number and become shorter, blunter, more or less serrated, partly fused, and often obsolescent. They commonly change from retrorse to antrorse, or become very irregular in orientation. Great care, therefore, must be taken in the identification of isolated fossil spines. In the present study, however, age variation is of no particular concern, since the two specimens are spines of large adults.

Ictalurus lambda, n. sp.

Pl. I, Figs. 2, 3; Pl. III

HOLOTYPE.—No. 6887, Museum of Natural History, University of Kansas, a left pectoral spine, with tip broken and ventral process (Pl. III Figs. 2, 3) lost; greatest length, 75.0 mm. (see Table I for measurements) Collected by Claude W. Hibbard, August 17, 1943.

REFERRED MATERIAL.—No. 6888, Museum of Natural History, University of Kansas, the base of a right pectoral spine, somewhat smaller than the holotype, with the processes broken; greatest length, 26.5 mm. Though it is imperfect, this specimen seems to agree satisfactorily with the holotype. It was collected by L. F. Phillis at the type locality, in association with a jaw of *Eucastor* and isolated teeth of *Nannippus* (Hibbard and Phillis, 1945) The few measurements that can be taken are included in Table I.


dorsal articulating surface
1
ventral facet
dorsal facet
dorsal articulating surface
2
anterior process
3
anterior edge
posterior process
posterior dentations
dorsal process
4

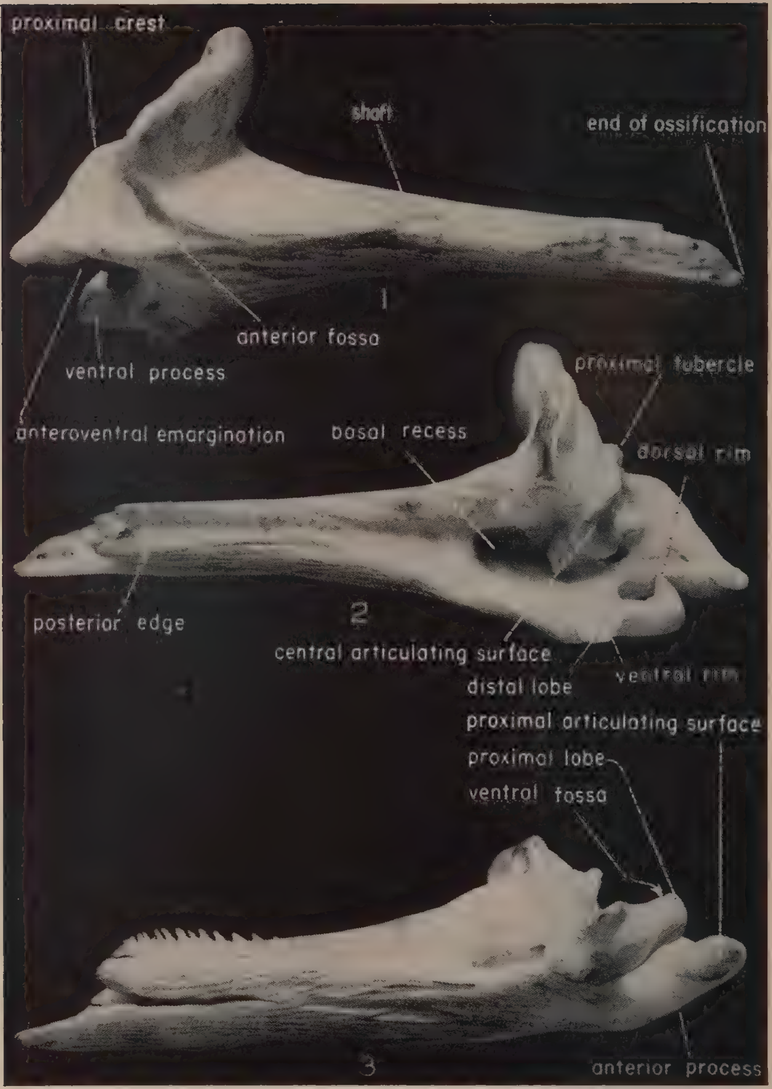
Left pectoral spines of *Ictalurus furcatus* and the holotype of *I. lambda*.

Fig. 1. Proximal view of pectoral spine of *Ictalurus furcatus* with ventral process blacked out to facilitate comparisons.

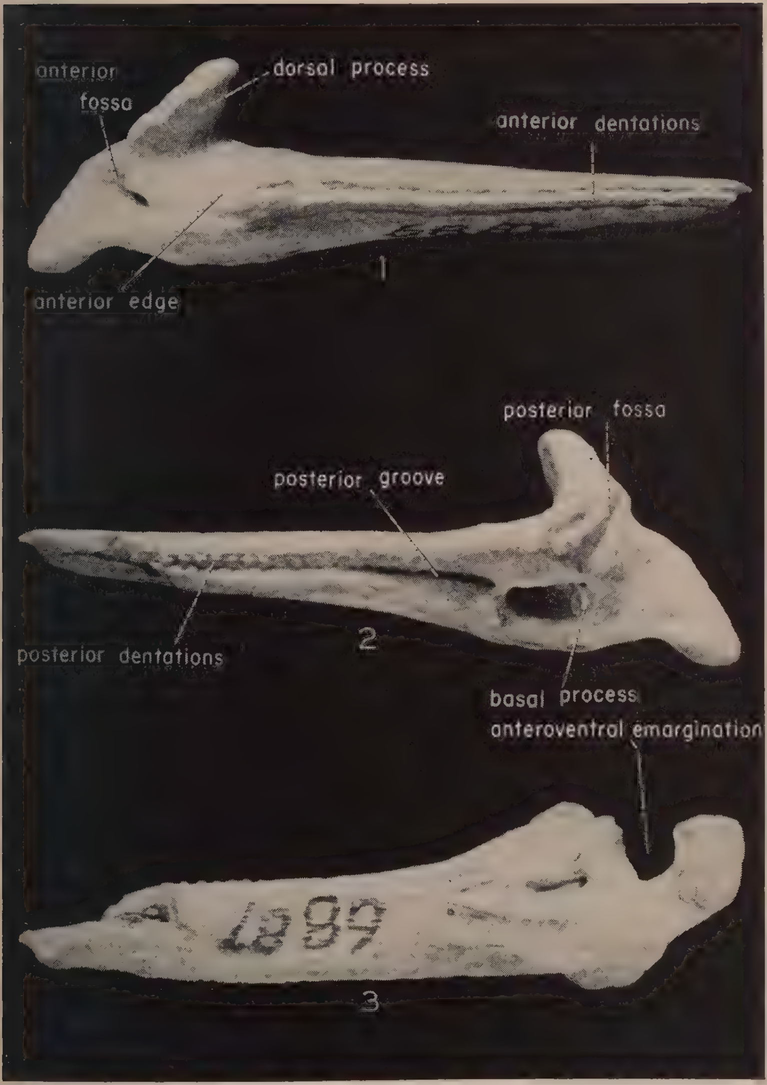
Fig. 2. Proximal view of pectoral spine of *Ictalurus lambda;* ventral process lacking.

Fig. 3. Dorsal view of left pectoral spine of *Ictalurus lambda.*

Fig. 4. Dorsal view of left pectoral spine of *Ictalurus furcatus.*


proximal crest
shaft
end of ossification
1
anterior fossa
ventral process
anteroventral emargination
proximal tubercle
basal recess
dorsal rim
posterior edge
2
central articulating surface
distal lobe
ventral rim
proximal articulating surface
proximal lobe
ventral fossa
3
anterior process

Left pectoral spine of *Ictalurus furcatus,* from Kansas River; spine 75.4 mm. long (also illustrated on Pl. I, Figs. 1 and 4).
Fig. 1. Anterior view.
Fig. 2. Posterior view.
Fig. 3. Ventral view.


anterior fossa
dorsal process
anterior dentations
anterior edge
1
posterior fossa
posterior groove
posterior dentations
2
basal process
anteroventral emargination
6887
3

Left pectoral spine of holotype of *Ictalurus lambda.*
Fig. 1. Anterior view.
Fig. 2. Posterior view.
Fig. 3. Ventral view.

The greatest length of the spine and the greatest distance between the margins of the dorsal and anterior processes are given in millimeters; the other measurements are expressed both in millimeters and as thousandths of the distance between the margins of these processes.

Character	*Ictalurus lambda* Type No. 6887	*Ictalurus lambda* No. 6888	*Ictalurus furcatus* Kansas River	*Ictalurus furcatus* Kansas River	*I. l. lacustris* Ohio	*I. l. lacustris* Lake Erie		*Pilodictis olivaris* Indiana
	Left spine	Right spine	Left spine	Right spine	Right spine	Left spine	Right spine	Left spine
Greatest length of spine	75.0*	26.5*	75.4*	97.8	63.1	67.6	60.2	67.1
Distance between margins of dorsal and anterior processes	31.2	....	33.9	32.6	16.5	20.2	20.8	20.2
Length of dorsal process	22.36 (717)	....	22.46 (663)	22.23 (682)	12.75 (773)	14.2 (703)	14.7 (707)	14.2 (703)
Elevation of dorsal process above base of spine	7.6 (244)	7.5	11.9 (351)	12.15 (373)	5.23 (317)	7.9 (391)	7.5 (361)	6.2 (307)
Width of dorsal process to nearest point of rim of central articulating surface	13.3 (426)	11.1	12.9 (381)	13.0 (399)	6.7 (406)	9.3 (460)	8.7 (418)	7.6 (376)
Height of anterior process above dorsal end of base of central articulating surface	17.1 (548)	....	20.6 (608)	19.6 (601)	8.8 (533)	11.2 (554)	12.0 (577)	12.3 (609)
Maximum width of proximal articulating surface†	10.0 (321)	....	5.8 (171)	6.2 (190)	4.3 (261)	5.1 (253)	5.4 (260)	5.9 (292)
Length of proximal articulating surface§	6.9 (221)	....	8.9 (263)	7.8 (239)	4.7 (285)	5.2 (257)	6.7 (322)	4.65 (230)
Distance between margins of anterior process and basal process	18.1 (580)	....	20.6 (608)	19.3 (592)	11.8 (715)	13.0 (644)	12.3 (591)	12.1 (599)
Width (near middle) of anterior fossa on anterior surface between dorsal and anterior processes	2.4 (77)	3.0	6.9 (204)	7.2 (221)	2.5 (152)	4.2 (208)	4.9 (236)	3.2 (158)
Width (anteroposterior) of spine‡	10.7 (343)	....	11.9 (351)	10.9 (334)	5.0 (303)	5.7 (282)	5.9 (284)	8.6 (426)
Dorsoventral width at same point	6.1 (196)	....	6.2 (183)	6.0 (184)	4.2 (255)	5.0 (247)	4.9 (236)	5.0 (247)
Length of posterior fossa	9.8 (314)	8.1	12.2 (360)	11.7 (359)	6.2 (376)	7.3 (361)	7.5 (361)	8.0 (396)
Width of posterior fossa	5.1 (163)	3.9	5.5 (162)	5.4 (166)	2.8 (170)	3.1 (153)	2.8 (135)	4.0 (198)
Length of central articular surface	8.2 (263)	8.0	11.0 (325)	12.4 (380)	6.7 (406)	7.8 (386)	7.4 (356)	10.35 (103)
Width of central articular surface	5.0 (160)	4.8	7.8 (230)	6.9 (212)	3.4 (206)	4.6 (228)	3.9 (188)	4.4 (218)
Length of basal recess (between outside rims)	9.4 (301)	8.0	11.8 (348)	12.5 (383)	7.1 (430)	8.8 (436)	9.1 (438)	13.2 (653)
Width of basal recess near middle	4.5 (144)	3.3	6.5 (192)	6.7 (205)	3.4 (206)	3.9 (193)	3.5 (168)	5.2 (257)
Greatest diameter of basal process	3.7 (119)	....	6.2 (183)	5.6 (172)	4.2 (255)	4.3 (213)	4.1 (197)	5.1 (252)
Height of basal process at anterior margin	1.7 (54)	....	2.7 (80)	2.6 (80)	0.9 (55)	0.8 (40)	0.5 (24)	2.9 (144)

* Spine broken

† Parallel to articulating surface, at right angles to the axis

§ In line with axis of spine

‡ At a distance, distal to basal recess, equal to distance between margins of dorsal and anterior processes, dentations included

Horizon and Type Locality.—Lower Pliocene, Ogallala formati Trego County, Kansas, locality No. 29 (of the University of Kansas), in t southwest corner of Sec. 15, T. 11 S., R. 22 W.

Description of Holotype.—In the following description of the holoty the spine structures are described in the sequence that is used in the precedi explanation of terminology.

The *anterior edge* is a definite ridge, with a rather deep marginal groo on each side and with numerous rather obscure dentations on the outer h (Pl. III, Fig. 1). The ridge is rather sharp, not rounded as it is in the ad of *Ictalurus furcatus* (Pl. II, Fig. 1), and the grooves are deeper and t dentations more definite. In *I. lacustris* these structures become obsolesce with age, though in the young the anterior edge is definitely denticula whereas in *I. furcatus* at like size the sharp anterior ridge is entire. *Pilodictis* the anterior dentations are unusually well developed in the adu In *Ameiurus* and in other catfishes these structures as well as the poster dentations are often characteristic of the species, as is indicated in t ichthyological literature (for example, for the Pimelodidae and for the Do didae by Eigenmann, 1917, pl. 35; 1925, pls. 2–27).

The *posterior dentations* are definite on the outer 1.5 cm. of the *poster* *edge,* as preserved (Pl. III, Fig. 2). They lie in a relatively deep *poster* *groove,* above the dorsal edge of which only the outer larger ones rise. T groove remains unusually distinct to its abrupt proximal end, only 2.0 m (in posterior projection) from the distal end of the basal recess. Small p and rugosities suggest that small dentations persisted to the proximal er In the adult of *I. furcatus* the dentations rise well above the dorsal rim the shallow posterior groove, which becomes very broad and indefinite at proximal end. In the adult of *I. lacustris* the dentations remain rather lar and the groove is poorly developed. In *Ameiurus* the conditions are variou In *Pilodictis* adults the posterior dentations are strong and definitely antror

The *basal recess* (Pl. III, Fig. 2) is comparatively small (Table I), b grades like a funnel into the hollow of the spine. In *I. furcatus* the dist opening into the hollow of the spine is smaller, and in *I. lacustris* the openi is a porelike foramen. In *Ameiurus* the condition is much as in *I. furcat* In *Pilodictis* the distal opening is very broad and in smaller specimens is co stricted by a cross ridge on the floor of the recess. In *Rhamdia* the openi into the middle of the spine is obsolescent. In the ariids at hand the openi is broad.

The *basal process* (Pl. III, Fig. 2) is a moderately elevated, concav topped peg, somewhat better developed than in *I. furcatus* and much high and sharper than in *I. lacustris.* In *Ameiurus* and *Pilodictis* it is moderate developed; in *Rhamdia* it is scarcely evident; in the ariids it is replaced a more or less developed but flat articulating surface.

The *central articulating surface* (Pl. III, Fig. 2) is relatively much small than in *I. furcatus* or *I. lacustris* (Table I). The *dorsal facet* is considerab larger than the *ventral facet.* The angle between the two flat surfaces about 25°. In the largest spines of *I. furcatus* this angle is 36° to 37° a the dorsal facet is concave. In smaller specimens and in all the spines

I. *lacustris* and of *Ameiurus* at hand, the surface is more groovelike and there is little differentiation into dorsal and ventral facets.

The rim of the central articulating surface is low, even on the *posterior process.* Weathering may be responsible, in part, for the lowness of the rim, but it is unlikely that the rim was ever high. It is moderately developed in recent species of *Ictalurus, Ameiurus* and *Pilodictis.* In *Rhamdia* the posterior process is a large knob, but elsewhere the rim is weakly developed. In the ariids the posterior process is variously developed. The anterior rim is obvious in *Bagre marinus,* but in *Galeichthys felis* and in *Selenaspis hertzbergi* the anterior rim is obsolescent, for the articulating surface grades into the proximal crest.

The *dorsal process* (Pl. III, Fig. 1) is less elevated above the dorsal face of the spine than it is in most species (Table I). The angle between the process and the spine is 75°. The concavity of the proximal surface is moderate. The *proximal tubercle* is inconspicuous. The edge of the process is narrowed and rounded transversely, not forming a flat band as it does in *Rhamdia* and in the Ariidae at hand.

The *posterior fossa* (Pl. III, Fig. 2) is pyriform, of moderate size (Table I), and rather deep: the walls in the outer part form an angle of about 115°; in the inner part of the trough, an angle of about 55°. The angulation on the axis is 162°. The narrower tip of the fossa ends abruptly at the base of the proximal surface of the process. A line across the rims of the fossa near its middle forms an angle of 45° with the tangent to the base of the spine. The axis of the basal part of the fossa forms an angle of 115° with the posterior groove. In the recent species of *Ictalurus* the posterior fossa is usually shallow and its axis forms more nearly a right angle with the posterior groove. In *Ameiurus* it is curved and is continued nearly to the tip of the posterior face of the dorsal process. In *Pilodictis* the posterior fossa is broad and is bent so sharply that the outer borders form approximately a right angle but the fossa ends in a rim well within the tip of the posterior face of the dorsal process. In *Rhamdia* the fossa is very shallow to obsolescent. In the ariids it is also very shallow.

The *anterior fossa* (Pl. III, Fig. 1) is very deep and very narrow (Table I). The width is sharply constricted by an angulation and tuberculation of the dorsal rim. At the tubercle the fossa is as deep as wide. The fossa continues as a shallow groove approximately in line with the axis of the spine. In *I. furcatus* (Pl. II, Fig. 1) the fossa is much broader and is very little constricted medially. In *I. lacustris* the shallow groove beyond the fossa is curved so as to continue along the anterodorsal face of the anterior process. In *Ameiurus* and *Pilodictis* the fossa approaches that of *I. furcatus.* In *Rhamdia* it is very shallow; in the ariids, it is moderately shallow.

The *proximal crest* (Pl. III, Fig. 1), about as in *I. lacustris,* is a massive, very low, little-curved ridge, that ends at the extreme base of the proximal face of the dorsal process. In *I. furcatus* (Pl. II, Fig. 1) it is narrower dorsally and is more arched. In *Ameiurus* the crest is much more arched and is rather strongly sigmoid. In *Pilodictis* it is high, narrow, and moderately sigmoid. The crest is very different in the Pimelodidae and the Ariidae, as repre-

sented by the specimens at hand. In *Rhamdia* it is a very short commissu
that extends from the dorsal process merely to the base of the anterior proce
In the ariids it is a high, thin, somewhat sigmoid crest that extends from t
tip of the anterior process well onto the proximal face of the dorsal proce

The *anterior process* (Pl. I, Fig. 2) is exceptionally massive (Table
As seen from the proximal face its axis is bent at an angle of 132°; from t
ventral face, 115°. The angle of the anterior rim is 120°. Because of t
sharp angulation, the process in ventral view (Pl. III, Fig. 3) is L-shap
(hence the specific name *lambda*). The angulation brings the long axis of t
articulating surface into an angle of 100° with the axis of the spine. In m
catfishes the two axes are on almost the same line. In *I. furcatus* and in
lacustris the articulating surface is little angulated. In *I. lacustris* it is som
what broadened. In *Ameiurus* there is a rather pointed expansion direct
posteriorly, not a broad squarish expansion as in *I. lambda*. In *Pilodictis* t
neck of the process is more slender in ventral view and the rounded artic
lating head is expanded anteriorly as well as posteriorly. In *Rhamdia* t
process is more compressed and is strongly hooked posteriorly. In the arii
the shape of the process is various. The characters of the ventral process a
indeterminate, as this process is missing in both specimens. It may be note
however, that *I. furcatus* differs from *I. lacustris* in the strongly upturn
dorsal rim of the proximal head (Pl. II, Fig. 2).

In so far as its characters are evident, specimen No. 6888 appears to
specifically referable to *I. lambda*. Most of the resemblances are reflected
the measurements (Table I). The posterior groove of the second specim
agrees with that of the holotype in being deep and narrow to the edge of t
basal recess. In both specimens the spine is rather finely striated and t
dorsal articulating surface (Pl. I, Fig. 2) is finely punctate.

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SCRIPPS INSTITUTION OF OCEANOGRAPHY (UNIVERSITY OF CALIFORNIA
LA JOLLA, CALIFORNIA, and DEPARTMENT OF GEOLOGY, UNIVERSITY
MICHIGAN, ANN ARBOR, MICHIGAN.

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Reprinted from PACIFIC SCIENCE, *vol. V, no. 1, January, 1951*

Record of the Shark *Carcharhinus longimanus*, Accompanied by *Naucrates* and *Remora*, from the East-Central Pacific[1]

CARL L. HUBBS[2]

THEIR MASTERLY TREATISE on the sharks
the western North Atlantic, Bigelow and
roeder (1948: 354–364, figs. 64–65), in
angling some complicated synonymies,
owed that the pelagic species commonly
own as *Carcharhinus lamia* (Risso) cannot
r this name, but should be called *C.*
gimanus (Poey). The literature is in such
nfusion that they were unable to verify the
currence of this species in any ocean other
n the Atlantic. It is therefore gratifying to
ain evidence promptly that it also inhabits
eastern tropical Pacific. This evidence is
vided in the form of a photograph of an
lt female specimen caught at Lat. 08° 16′
Long. 125° 43′ W., by A. J. Carsola and
emiah F. Black of the United States Navy
ctronics Laboratory, on the ship "Serrano."[3]
s picture (Fig. 1) corresponds very closely
h Bigelow and Schroeder's figure of an
lt female, especially in the highly diagnos-
features of the broadly rounded first dorsal
the markedly enlarged and round-tipped
toral fin, the convex posterior border of the
er caudal lobe, the size and position of
anal and second dorsal fins, the extremely
rt snout in front of the nostrils, and the
oration. There can be virtually no doubt as
he identification.

The lack of previous records from the eastern Pacific (see Beebe and Tee-Van, 1941, and Fowler, 1944) is explicable, for nearly all previous collecting has been near shore, and Bigelow and Schroeder indicate that this species is more strictly pelagic than any other in the Atlantic and is more definitely tropical than most of them. The new Pacific record station lies far off Mexico and east-southeast of the Hawaiian Islands.

The circumstances of the capture of the Pacific specimen are given in the log of the "Serrano," as follows:

> 27 May 1949, 1516 PST. A gray shark with white fin and tail tips was observed swimming around the ship about this time; three fish, each about one foot long and decorated by transverse black and silver stripes maintained formation with the shark, one being about a foot in front of him, another just below his body mid-section and another just above him. The shark was baited with a light hook and line, shot, and pulled onto deck (see picture).

The banded fish were of course *Naucrates ductor* (Linnaeus). Like the *Carcharhinus* that they were accompanying, the pilotfish are referable to a circumtropical species. It is true that Fowler (1905: 62–65, fig. 3) described the Pacific form as a distinct species, *Naucrates polysarcus*, partly on the basis of differences pointed out by Gill (1862: 440–441), but it now seems likely that the distinction was based on juvenile characters. The supposedly deeper body and the longer fins may well be characters of the young. Meek and Hildebrand (1925: 401) stated that "the

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ontributions from the Scripps Institution of Ocean-
phy, New Series, No. 493. Manuscript received
ruary 1, 1950.

rofessor of Biology, Scripps Institution of Ocean-
phy, University of California, La Jolla.

hanks are due E. R. Anderson of the United States
y Electronics Laboratory for the transmission of
, photograph, and specimen.

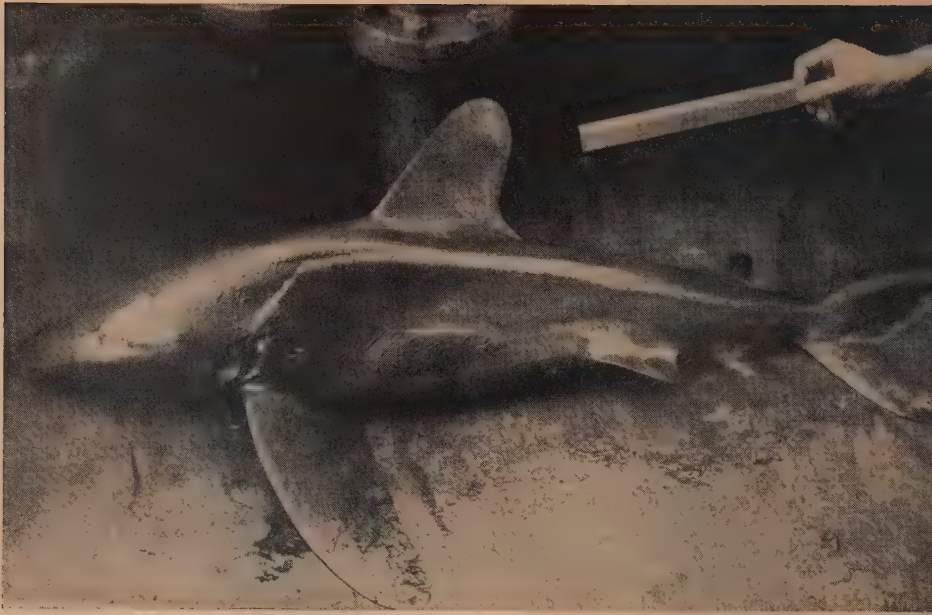

FIG. 1. Adult female of *Carcharhinus longimanus* (Poey), from the east-central Pacific. OFFICIAL PHOTOG
U. S. NAVY.

young appear to be deeper and more strongly compressed than the adult"; Wakiya (1924: 232, pl. 38, fig. 2), however, indicated that the young of "*Naucrates indicus*" are more slender than the adult. The original figure of *N. polysarcus* suggests that the extreme depth ascribed to the type may be attributed to its poor preservation. The different scale count, also emphasized by Fowler, is probably not significant, for the scales are too irregularly arranged to be counted precisely. Jordan and Starks (1907: 72) found that the supposed characters do not hold for a Pacific species, and Meek and Hildebrand, though failing to include *polysarcus* in their synonymy, refer Pacific material to *N. ductor*. Walford (1937: 66–68) likewise referred the Pacific form to *N. ductor* (and by mistake labeled the figure, which was taken from Jordan and Evermann, as "from Jordan and McGregor, 1898"). An adult specimen 325 mm. in standard length, recently received from off the Pacific coast of Mexico, has the slender form and the short fins ascribed by Fowler to the Atlantic
Recently, Fowler (1944: 423, 500) tr
polysarcus as a subspecies of *ductor*.

From the shark there was taken a speci
105 mm. long, of another circumtro
species, *Remora remora* (Linnaeus). It a
satisfactorily with material from sou
California.

The specific integrity of such cir
tropical pelagic fishes poses a proble
speciation, since widespread littoral typ
the tropics, as well as most pantemp
types, in contrast, are ordinarily different
into allopatric subspecies or species, th
their period of isolation has ordinarily
no longer, often briefer, than that of the
separated populations of the tropical pe
forms. The explanation seems to lie bo
the uniformity of the tropical pelagic
vironment and in the relationship betwee
population structure and the rate of sp
tion. Large, widespread populations tha
not disrupted into effective reproductive

now generally held, on the basis of
ght's analyses (1940*a*, *b;* 1942), to be
e subject to differentiation.

ADDENDUM

fter this manuscript was submitted for
lication, Springer (1950: 2, 7–8) erected a
inct genus, *Pterolamia*, for the reception of
charhinus longimanus and, probably also, of
insularum (Snyder), a species described
n the Hawaiian Islands. He separated this
inal genus from *Eulamia* solely on the
s of the rounded tips of the dorsal and
toral fins. Since the sharpness of these fins
es considerably and since the rounded
seem to involve merely the retention of
embryonic feature, I am disinclined to ac-
the generic separation. Some other
cies of *Carcharhinus*, for example, *C. falci-*
is (Müller and Henle) as described by
elow and Schroeder (1948: 329–333, figs.
57), have the pectoral scarcely more
nted than in *C. longimanus* and have the
sal distinctly though less broadly rounded.
does Springer's separation of *Eulamia*
n *Carcharhinus* seem justified on the basis
he presence or absence of a middorsal
e—a very tenuous distinction that de-
ds in large part on the condition of preser-
on and that seems to be inconsistent, in
e species at least.

hat *Carcharhinus longimanus* may be com-
n in the open equatorial Pacific is sug-
ted by a picture in the recently published
k *Kon-Tiki*, showing nine sharks caught
ne day (Heyerdahl, 1950: lower figure of
pl. following p. 176; accompanying text
arently on pp. 205–206). So far as is ob-
s all sharks in this picture seem referable
he pelagic species under discussion. This
tification is ventured on the basis of the
wing of certain diagnostic characters, in
icular the broadly rounded pectoral fins,
h longer than the head; the far-forward
tion of the nostrils on the very short,
ngly rounded, laterally angulated snout;
the plain coloration. The location of the
catch is not specified, but the context indicates that it was in the South Equatorial Current somewhere between Perú and the Tuamotu Archipelago.

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POPULATION STUDIES, LOCAL GROWTH RATES AND REPRODUCTION OF THE PISMO CLAM
(*Tivela stultorum*)

By

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AND

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ABSTRACT

Large samples collected, measured, and returned to the beach at monthly intervals at La Jolla, California, for five successive years showed an average initial set of 3 young clams per sq m in an area of 2000 sq m. The annual mortality has been from 67 to 75% for each year-class. Of an annual set of 6000, only 2000, 700, 170 and 50, respectively, have remained at the end of the first to fourth years. The length increases about 21 mm per year for the first two years of life and somewhat less thereafter. Less than one per cent survived long enough to reach the legal length of 127 mm.

In the cooler waters of three more northern localities investigated, growth is more rapid, average length of life is longer, and large crops of legal size are produced annually. Population studies by the California Bureau of Marine Fisheries at Pismo Beach for 19 years showed that an average of 50% of those not more than four years old belonged to the first year-class and 23, 13 and 14%, respectively, to the second, third and fourth year-classes. Wide fluctuations occurred. In some years only 0 to 10% of the population belonged to the first year-class, while in other years this year-class comprised 60 to 80%.

The most productive areas on both the California and Mexican coasts are those with extensive upwelling of cool oceanic water, bringing inorganic nutrients essential for the growth of phytoplankton. The principal spawning season is June to December.

The natural populations of this species, which is one of the largest and most palatable of the bivalves on the California coast, have been studied by collecting samples at monthly intervals for five successive years, 1945–1950, on the beach at the Scripps Institution of Oceanography at La Jolla, California. Many marked individuals were also replanted on the beach and remeasured monthly. In addition to this local population, less frequent studies have been made at other localities along the coast for a number of years with the object of determining the population changes from year to year, the sizes and ages of the constituent year-classes, the rates of growth at each locality, the season

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[1] Contribution from the Scripps Institution of Oceanography, New Series No. 495.

Reprint from SEARS FOUND. JOURN. MAR. RES.

of spawning and the date of the first appearance of the young clams on the beach.

The Pismo clam inhabits the open coast of the southern half of California and most of the Pacific coast of Lower California. Because of its economic importance, this species has been investigated extensively under the auspices of the California Division of Fish and Game. Weymouth (1923) published a detailed report of its habits, growth and economic aspects. This report was supplemented by Herrington (1930) and population statistics have been published by Clark (1932), Roedel (1939), Aplin (1947), and others. The rates of growth at La Jolla and the nature of the food and its digestion, as well as the sexuality, were described by Coe (1947, 1948), while Fitch (1950) has published a popular account of the ecology, growth and utilization of the clam and the management of the fishery.

In order to determine the extent to which local conditions influence the populations, productivity, rates of growth and the spawning season, collections have been made during each month of the year, with a few exceptions, at four widely separated localities along the coast. The most southern of these are La Jolla and La Jolla Shores, the most northern Pismo Beach, the two being separated by about 215 miles of seacoast. Sunset Beach is about 65 miles northwest of La Jolla, Point Hueneme 65 miles northwest of Sunset Beach, and Pismo Beach about 85 miles further northwest. The season of development of the sexual products and the spawning periods at each of these localities, as well as at Morro Bay and at several beaches on the coast of Lower California, were also investigated. The writers are indebted to Professor and Mrs. Carl L. Hubbs for material and temperature records from some of these more southern localities and to the Bureau of Marine Fisheries for permitting the inclusion of data on the yearly variations in the populations at Pismo Beach obtained by the California Division of Fish and Game.

The constituents of the population and the average lengths of the clams in each of the first four year-classes at each of these localities in samples collected at monthly intervals are shown in Tables I to XIII. The figures given indicate the averages for five years at La Jolla, two to three years at La Jolla Shores, Sunset Beach and Hueneme, and 19 years at Pismo Beach. The mean lengths represent the weighted averages for all of the collections in the corresponding months of successive years. The number of individuals on which the data are based and the average temperature are included.

As an introduction to the present report it may be stated that these clams are generally of separate sexes, with less than one per cent ambisexuality. Weymouth (1923) erroneously reported them as being hermaphroditic. The principal spawning season extends from June to December, although some individuals may not complete spawning until January and a few may spawn at intervals during the remainder of the year. At La Jolla many of the young clams spawn at the age of about one year, when they are 17 to 31 mm in length, but most of those with retarded growth first become sexually mature in their second summer. At the more northern of the localities investigated, spawning is usually delayed until the clam's second summer or autumn. The older individuals have a prolonged spawning season, discharging their sexual products at intervals during two to six months or more. The ova are very small, measuring only 0.074 to 0.081 mm in diameter, exclusive of the gelatinous membrane, but they are produced in great numbers. A large female may liberate from 10 to 20 million eggs each year for five or more years (Coe, 1947).

After completion of a free-swimming larval period, the minute young clams settle on the beach and remain there unless disturbed by the surf or by enemies. The period of the most successful settling and survival of the young may occur early in the season or one to six months later. Consequently it is usual that in any year-class some individuals are several months older than others.

The constituent year-classes in the population have varied considerably from year to year due to differences in the initial set of young clams and the subsequent mortality. At La Jolla there has been an annual loss of 67 to 75% for each year-class, and less than one per cent of the young clams reached the age of four years. At Pismo Beach, where the water is cooler in summer and conditions for survival much better, the losses have been estimated as 55, 45, 29, 34, 52, 68 and 72%, respectively, for the first to seventh years. The sharp increase in the fifth to seventh years is attributable to the taking of clams of legal size for food. An average of only one clam in each 200 of the original set remains.

The causes, other than human agencies, of this high rate of mortality have not been fully determined. Many of the clams are killed by gulls and others by various species of sharks, rays and bony fishes. Others are drilled by boring snails and some are devoured by cancer crabs, but the highest mortality usually occurs in summer when dinoflagellates are most abundant. At such times vast numbers of clams, particularly those of the first and second year-classes at La Jolla, die from unexplained causes. Dying clams and empty shells may then be left in rows along the shore. Possibly unfavorably high temperature or "disease" may be among the contributing factors. Trematode parasites are common, especially in the older clams, but they are not considered to be seriously detrimental.

During some years the set of young clams on a particular beach has been an almost complete failure and one or more year-classes have been missing from the subsequent population. But whether the mortality has occurred during the larval period or after the settlement of the delicate young clams on the beach at times of heavy surf has not been determined.

Growth is slower than in many bivalves, the average increase at La Jolla being between 21 and 22 mm a year during the first two years of life and somewhat less thereafter (Fig. 1). The legal length of 5 inches is reached in about seven years, while the largest individuals known from La Jolla were 148 to 151 mm long, with an estimated age of 10 years or more. At other localities, lengths of 170 to 175 mm have been found and the age has been estimated as 18 to 25 years. The most rapid increase in length usually occurs during the clam's second year (Table XIII), but the volume and weight increase more rapidly thereafter (Coe, 1947).

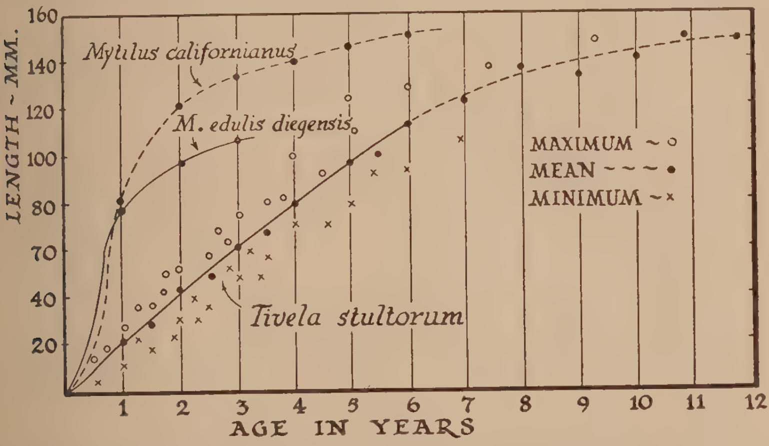

Figure 1. Growth curve of the Pismo clam at La Jolla. Corresponding curves of the growth of the sea-mussel and the bay-mussel from the pier adjacent to the clam beds are indicated for comparison.

Like most other bivalve mollusks, these clams are typical ciliary and mucous feeders, taking into the stomach a great variety of small particles. These include not only living and dead organic materials but also a considerable proportion of sand and small fragments of mollusk shells. The organic material consists mainly of diatoms, dinoflagellates and other unicellular algae, as well as other phytoplankton, both living and dead, protozoans, microflagellates and bacteria. Detritus derived from the decomposed tissues of all species of marine animals and plants is evidently an important part of the clam's nutrition. However, the experimental studies by Coe (1947, 1948) have shown that only the smallest of these particles and cells without cellulose walls can actually be digested.

INVESTIGATIONS AT LA JOLLA

Collections containing usually about 200 individuals were made near the end of each month, with a few exceptions, during each of the five years. After being measured, the clams were returned to the same part of the beach from which they had been taken. In so far as possible the same individuals were collected in each succeeding month, although most of those that represented the first year-class in 1945 had disappeared before the end of the experimental period in 1950. The number of individuals and the average length and range of those in each year-class for the corresponding months of each year are shown in Tables I and II. It will be noted that the most rapid growth occurs from May to September. During that period the phytoplankton is most abundant and the temperature is highest (Fig. 2). During the winter the growth rate is inhibited by the lower temperature, rougher seas, shifting sand and less abundant nutrition.

The area included in the population studies at La Jolla covered about 2000 square meters of the beach at the Scripps Institution, legally protected from human interference. It is estimated that an average of three young clams arrived on each square meter each year, but the annual decrease in the population has been from 67 to 75% for each year-class. Most of this decrease has been due to destruction by enemies or to death from natural casuses, but a few of the clams were taken by poachers and a relatively small number were carried by the surf into deeper water. Of the average annual set of approximately 6000, only about 2000, 700, 170 and 50 respectively remained at the end of the first to fourth years. The proportions actually collected were 1008, 347, 83 and 25. The constituents of the population found at the end of each month in 1946–47 and the changes which occurred during the year are shown by the diagrams in Fig. 3.

Rates of Growth. In computing the average of the collections at the end of September of these five years, it is found that the 1008 individuals estimated to have an average age of one year had a mean length of 21.5 mm. The lengths varied from 11 to 31 mm (Table I), indicative not only of variations in growth rate but also of differences in actual age because of the prolonged spawning season and the different times of settlement on the beach.

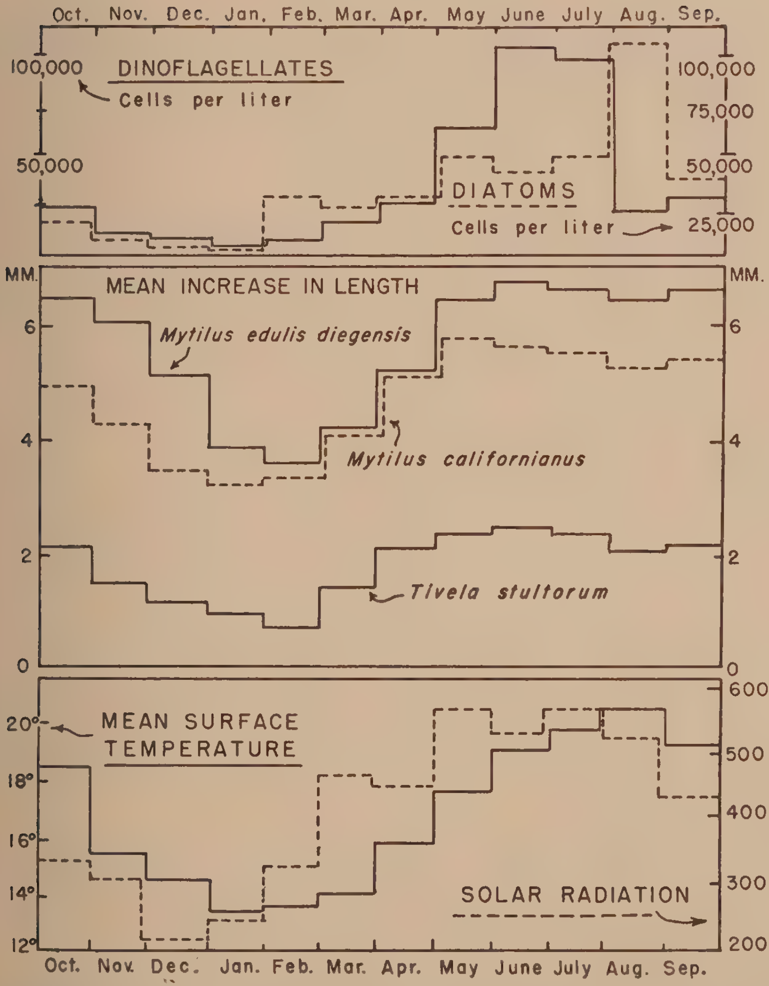

Figure 2. Correlation between temperature, solar radiation, abundance of dinoflagellates and diatoms and mean monthly increase in length at La Jolla during the two years 1945–47. The growth rates are more nearly parallel with the abundance of dinoflagellates than with the other environmental conditions. The incident solar radiation is shown in terms of g. cal./cm²/day. Corresponding curves for the two species of mussels growing on the piles adjacent to the clam beds are indicated for comparison.

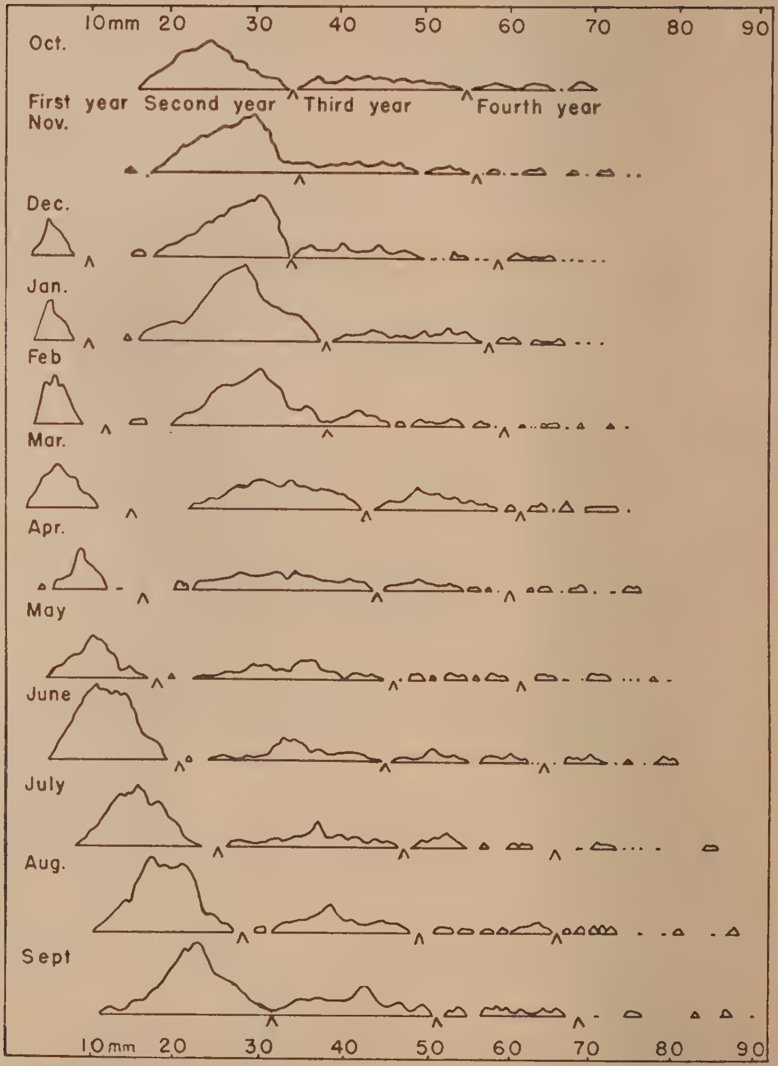

Figure 3. The length-frequency of the first four year-classes in the population at La Jolla during the year 1946–47. as determined from samples collected at the end of each month, October to September. The high mortality is indicated by the rapidly decreasing numbers in each year-class.

At an estimated average age of two years the mean length of 347 individuals had increased to 42.8 mm, indicating an increase of 21.3 mm during the second year. This is only slightly less than during the first year. The relative number of individuals two years old in the population, however, had decreased to but little more than a third of those found in the first year-class. The maximum length at the end of the second year was 52 mm and the minimum 29 mm (Table I).

TABLE I.—RATES OF GROWTH AT LA JOLLA DURING FIRST AND SECOND YEARS

Date	*Average water temperature*	*Average age, months*	*Number in samples*	*Length, mm*		*Indicated increase in month*
				Mean	*Range*	
October	18.26	1	—	—	—	—
November	15.58	2	—	—	—	—
December	14.15	3	368	4.8	3–7	—
January	13.08	4	145	5.6	4–12	0.8
February	13.11	5	107	6.5	4–12	0.9
March	13.84	6	457	7.6	4–13	1.1
April	15.28	7	144	9.4	4–18	1.8
May	17.36	8	491	11.7	5–22	2.3
June	18.88	9	813	14.3	6–22	2.6
July	19.57	10	1016	16.7	7–26	2.4
August	20.48	11	1183	19.0	11–30	2.3
September	19.64	12	1008	21.5	11–31	2.5
October	18.26	13	217	23.4	15–33	1.9
November	15.58	14	602	25.0	15–35	1.6
December	14.15	15	548	26.4	15–38	1.4
January	13.08	16	646	27.4	17–39	1.0
February	13.11	17	514	28.5	15–39	1.1
March	13.84	18	521	30.1	17–41	1.6
April	15.28	19	434	32.4	22–43	2.3
May	17.36	20	362	33.7	20–45	1.3
June	18.88	21	281	36.0	22–46	2.3
July	19.57	22	273	38.2	24–49	2.2
August	20.48	23	184	40.4	28–50	2.2
September	19.64	24	347	42.8	29–52	2.4

In the collections made at the end of September, 1945–1949, only 83 individuals were found with an estimated age of three years. Their average length was 62.0 mm, indicating a mean increase of 19.2 mm during the third year. The maximum was 68 mm and the minimum 52 (Tables II and III).

At the average age of four years the lengths varied between 67 and 95 mm, with a mean of 78.9 mm, indicating an increase of 16.9 mm during the fourth year (Table III).

Marked Individuals. A reliable measurement of the growth rates from month to month was obtained by marking the shells of more than 800 clams and replanting them on the beach. From those that were recovered subsequently it was found that the average increase in

TABLE II.—RATES OF GROWTH AT LA JOLLA DURING THIRD AND FOURTH YEARS

Date	*Average water temperature*	*Average age, months*	*Number in samples*	*Length, mm*		*Indicated increase in month*
				Mean	*Range*	
October	18.26	25	73	44.6	31–53	1.8
November	15.58	26	94	45.9	35–55	1.3
December	14.15	27	106	47.1	35–55	1.2
January	13.08	28	92	47.0	35–56	−0.1
February	12.11	29	104	48.1	38–59	1.1
March	13.84	30	128	50.3	39–62	2.2
April	15.28	31	91	52.1	42–58	1.8
May	17.36	32	76	54.1	44–61	2.0
June	18.88	33	68	56.3	46–63	2.2
July	19.57	34	64	58.4	49–65	2.1
August	20.48	35	61	60.1	50–65	1.7
September	19.64	36	83	62.0	52–68	1.9
October	18.26	37	37	63.1	57–69	1.1
November	15.58	38	29	64.1	57–78	1.0
December	14.15	39	26	64.0	60–70	−0.1
January	13.08	40	23	65.8	59–71	1.8
February	13.11	41	28	66.9	59–73	1.1
March	13.84	42	24	68.4	62–74	1.5
April	15.28	43	25	70.3	62–76	1.9
May	17.36	44	24	72.4	63–79	2.1
June	18.88	45	24	74.4	64–80	2.0
July	19.57	46	19	76.2	66–86	1.8
August	20.48	47	20	76.9	67–89	0.7
September	19.64	48	25	78.9	67–95	2.0

TABLE III.—RELATIVE PROPORTIONS OF THE POPULATION IN EACH AGE GROUP AND YEARLY INCREMENT IN LENGTH (mm) AT LA JOLLA IN FIRST, SECOND, THIRD AND FOURTH YEARS, AS ESTIMATED FROM SAMPLES COLLECTED AT END OF SEPTEMBER IN EACH YEAR

Year	*Av. age, 1 year*		*Av. age, 2 years*			*Av. age, 3 years*			*Av. age, 4 years*		
	No. in sample	*Av. length*	*No. in sample*	*Av. length*	*Inc.*	*No. in sample*	*Av. length*	*Inc.*	*No. in sample*	*Av. length*	*Inc.*
1945	135	20.9	38	42.0	—	21	58.5	—	3	77.3	—
1946	247	21.2	61	42.3	21.4	12	61.8	19.8	3	78.4	19.9
1947	214	21.4	71	41.1	19.9	8	59.1	16.8	4	81.1	19.3
1948	211	20.7	82	43.1	21.7	19	62.0	20.9	6	75.2	16.1
1949	141	23.3	95	45.3	22.2	23	68.6	19.3	9	82.4	12.3
Total	1008	—	347	—	—	83	—	—	25	—	—
Aver.	—	21.5	—	42.8	21.3	—	62.0	19.2	—	78.9	16.9

length in their second and third years was 2.1 mm in October, 1.7 mm in November, 1.2 mm in December, 0.9 mm in January, 0.7 mm in February, 1.2 mm in March, 2.0 mm in April, 2.3 mm in May, 2.4 mm in June, 2.3 mm in July, 2.0 mm in August, and 2.3 mm in September. These figures indicate an increase of only 7.8 mm for the six months preceding the end of March and 13.3 mm during the following half year, the increment for the entire year being 21.1 mm (Fig. 2). This would average 1.3 mm per month in winter and 2.2 mm per month in summer.

INVESTIGATIONS AT LA JOLLA SHORES

On this beach, which is only a mile from the one at the Scripps Institution, there has been only occasional patrol by the wardens of the California Division of Fish and Game and this has not prevented the public from taking as many young clams of illegal size as could be found. Consequently there is a less natural population and the collections, which were made at intervals over several years, show much less uniformity. The temperature and other environmental conditions at the two localities are essentially similar, except that in spite of the relatively large numbers in the first and second year-classes only a few individuals have been permitted to reach their third year and nearly all have been taken from the beach before the end of their fourth year (Tables IV and V). The population has been maintained by the spawning of such young individuals as have escaped the public and by older ones living in deeper water or on other beaches.

TABLE IV.—RATES OF GROWTH AT LA JOLLA SHORES DURING FIRST AND SECOND YEARS

Date	*Average age, months*	*Number in samples*	*Length, mm*		*Indicated increase in month*
			Mean	*Range*	
October	1	—	—	—	—
November	2	—	—	—	—
December	3	8	7.2	5–9	—
January	4	33	8.5	4–13	1.3
February	5	83	8.1	2–13	−0.4
March	6	13	10.8	6–17	2.7
April	7	38	10.1	7–17	−0.7
May	8	317	9.7	3–22	−0.4
June	9	241	11.7	2–24	2.0
July	10	686	11.1	3–25	−0.6
August	11	330	14.3	6–27	3.2
September	12	234	20.2	13–20	5.9
October	13	467	19.9	9–34	−0.3
November	14	473	21.5	11–36	1.6
December	15	464	24.6	10–38	3.1
January	16	446	25.5	14–40	0.9
February	17	258	28.3	15–42	2.8
March	18	80	31.2	23–39	2.9
April	19	116	31.0	19–45	−0.2
May	20	212	34.0	21–45	3.0
June	21	103	36.9	29–48	2.9
July	22	261	38.6	26–48	1.7
August	23	278	39.7	25–53	1.1
September	24	87	40.8	31–53	1.1

The average lengths at the end of the first, second and third years were 20.2, 40.8 and 63.7 respectively at La Jolla Shores as compared with 21.5, 42.8 and 62.0 mm at La Jolla. These small differences do not exceed the probable errors to be expected in random samples (Tables IV and V).

TABLE V.—RATES OF GROWTH AT LA JOLLA SHORES DURING THIRD AND FOURTH YEARS

Date	*Average age, months*	*Number in samples*	*Length, mm*		*Indicated increase in month*
			Mean	*Range*	
October	25	290	40.4	29–58	−0.3
November	26	103	42.3	32–63	1.9
December	27	72	44.0	34–56	1.7
January	28	95	47.2	38–61	3.2
February	29	49	49.9	44–63	2.7
March	30	19	45.4	41–55	4.5
April	31	34	53.2	46–61	7.8
May	32	47	50.9	44–59	−2.3
June	33	13	58.6	51–66	7.7
July	34	55	54.5	47.68	−4.1
August	35	29	60.0	51–68	5.5
September	36	15	63.7	56–77	3.7
October	37	54	61.2	53–81	−2.5
November	38	8	63.6	59–68	2.4
December	39	2	64.5	63–66	0.9
January	40	5	66.6	59–81	2.1
February	41	5	71.0	67–78	4.4
March	42	—	—	—	—
April	43	—	—	—	—
May	44	—	—	—	—
June	45	5	73.6	68–81	—
July	46	2	79.5	71–88	5.9
August	47	6	72.8	71–75	−6.7
September	48	—	—	—	—

In some months the collections on the two beaches were nearly identical, while in other months there was a wide difference in the proportions of the year-classes. One curious difference deserves special emphasis. A comparison of Tables I and IV shows that some individuals of the first year-class only 3 mm in length continued to be found as late as July at La Jolla Shores, while none of that small size have been discovered at La Jolla later than the preceding December. A length of 3 mm would normally indicate an individual less than two months after setting, giving evidence that spawning may occasionally continue as late as March or April. At that time the gonads of most of the population are in various stages of gametogenesis preparatory to the more usual spawning season, June to December.

INVESTIGATIONS AT SUNSET BEACH

This locality, about 65 miles northwest of La Jolla, has been particularly favorable for the rapid growth of the clam, presumably because of the large sewer which brings to the vicinity an abundance of nutrients from the wastes of a dense human population. The temperature of the water at nearby Balboa Pier averages only slightly lower than that at La Jolla (Tables VI, VII and XIII). The mean length at the estimated average age of one year was found to be 26.9

TABLE VI.—RATES OF GROWTH AT SUNSET BEACH DURING FIRST AND SECOND YEARS

Date	*Average water* temperature*	*Average age, months*	*Number in samples*	*Length, mm*		*Indicated increase in month*
				Mean	*Range*	
October	16.72	1	—	—	—	—
November	15.07	2	—	—	—	—
December	13.76	3	—	—	—	—
January	12.13	4	—	—	—	—
February	12.31	5	3	5.3	4–6	—
March	12.96	6	—	—	—	—
April	14.37	7	1	8	8	—
May	17.19	8	208	7.3	4–20	−0.7
June	19.05	9	557	13.4	5–27	6.1
July	18.95	10	127	14.0	6–25	0.6
August	19.24	11	141	21.0	16–32	7.0
September	18.62	12	128	26.9	19–35	5.9
October	16.72	13	284	30.9	21.45	4.0
November	15.07	14	204	21.7	24–41	0.8
December	13.76	15	279	36.8	21–49	5.1
January	12.13	16	162	34.5	21–49	−2.3
February	12.31	17	140	37.6	27–43	3.1
March	12.96	18	—	—	—	—
April	14.37	19	20	42.3	36–51	—
May	17.19	20	202	47.0	40–57	4.7
June	19.05	21	278	53.8	42–75	6.8
July	18.95	22	316	57.6	42–70	3.8
August	19.24	23	54	61.5	47–70	3.9
September	18.62	24	133	65.2	46–77	3.7

* At Balboa Pier, 1948–49

mm, as compared with 21.5 mm at La Jolla. The average length at the estimated age of two years was 65.2 mm, as compared with 42.8 at La Jolla, while those clams believed to be three years old averaged 88.5 mm, with a maximum of 102 mm. During the fourth year the lengths varied from 78 to 122 mm, with an average of 103.8 mm at the end of the year (Table VII).

These data would indicate an average increase of 26.9 mm during the first year, 38.3 mm in the second, 23.3 mm in the third, and 15.3 mm in the fourth year (Table XIII). This last figure is obviously not representative, since it was based on only 6 individuals and is smaller than indicated for the same year-class three months earlier (Tables VI and VII). The disappearance of this year-class is attributed to removal of clams of both legal and illegal sizes from this beach by the public.

To determine whether the rapid growth rate was due to the environmental conditions or to different genetic factors in the population, more than 100 individuals were marked as to size and transplanted from this beach to La Jolla at various times. They grew somewhat more rapidly for two or three months than clams of similar size in the native population near which they were planted. However, after a few months those from Sunset Beach grew no faster than their native

TABLE VII.—RATES OF GROWTH AT SUNSET BEACH DURING THIRD AND FOURTH YEARS

Date	*Average water* temperature*	*Average age, months*	*Number in samples*	*Length, mm*		*Indicated increase in month*
				Mean	*Range*	
October	16.72	25	170	67.0	50–77	1.8
November	15.07	26	68	65.0	53–79	−2.0
December	13.76	27	278	70.1	50–82	4.9
January	12.13	28	244	70.1	54–88	0.0
February	12.31	29	283	70.1	55–88	0.0
March	12.96	30	—	—	—	—
April	14.37	31	154	73.0	59–88	—
May	17.19	32	427	75.0	58–91	2.0
June	19.05	33	294	78.4	64–94	3.4
July	18.95	34	226	82.8	69–97	4.4
August	19.24	35	256	85.2	74–99	2.4
September	18.62	36	243	88.5	69–102	3.3
October	16.72	37	197	89.2	78–101	0.7
November	15.07	38	26	93.7	79–103	4.5
December	13.76	39	347	95.6	82–116	1.9
January	12.13	40	137	96.9	85–115	1.3
February	12.31	41	145	96.5	84–115	−0.4
March	12.96	42	—	—	—	—
April	14.37	43	135	100.7	89–122	—
May	17.19	44	120	99.5	87–118	−1.2
June	19.05	45	94	104.1	92–121	4.6
July	18.95	46	94	103.1	92–117	−1.0
August	19.24	47	—	—	—	—
September	18.62	48	6	103.8	97–110	—

* At Balboa Pier, 1948–49

associates. It is therefore concluded that the increased growth rate of the population at Sunset Beach results from the favorable environmental conditions and not from different hereditary characteristics.

Although the spawning season is approximately the same as that at La Jolla, no representatives of the new set have been found until February and only four individuals until May. The size in the latter month (4 to 20 mm) obviously indicates a group present earlier but previously overlooked. All were fully ripe or partly spawned out in August.

INVESTIGATIONS AT POINT HUENEME

Point Hueneme is only about 130 miles northwest of La Jolla, but the temperature of the water is generally considerably lower. The differences vary with the season, and in most years the temperatures are only 1 to 2° C lower than those at La Jolla during the winter but are commonly 3 to 4° lower during the summer and autumn months when most of the clams are spawning and when they have the most rapid rate of growth (Tables VIII and IX). These temperatures were taken on the open coast, however, and are several degrees lower than those at the clam beds on sunny afternoons.

Nevertheless, it would appear that the clams increase in size more rapidly than at any of the other localities with the exception of Sunset Beach (Tables VIII and IX). It seems probable that the low summer temperatures indicate the upwelling of oceanic water, bringing to that area inorganic nutrients favorable for an initial growth of phytoplankton and indirectly for the microorganisms and detritus on which the clam's nutrition depends. The average spawning season is about two months later than at La Jolla.

TABLE VIII.—RATES OF GROWTH AT POINT HUENEME DURING FIRST AND SECOND YEARS

Date	*Average water* temperature*	*Average age, months*	*Number in samples*	*Length, mm*		*Indicated increase in month*
				Mean	*Range*	
December	12.95	1	—	—	—	—
January	11.10	2	—	—	—	—
February	11.43	3	—	—	—	—
March	12.25	4	—	—	—	—
April	13.05	5	—	—	—	—
May	14.80	6	—	—	—	—
June	15.03	7	46	10.2	4–15	—
July	16.30	8	120	9.0	4–21	−1.2
August	16.04	9	225	13.0	5–28	4.0
September	16.61	10	—	—	—	—
October	15.34	11	1	22.0	22	—
November	14.82	12	35	23.4	11–32	1.4
December	12.95	13	—	—	—	—
January	11.10	14	208	35.0	20–44	—
February	11.43	15	200	38.6	28–49	3.6
March	12.25	16	—	—	—	—
April	13.05	17	152	41.3	33–52	—
May	14.80	18	153	46.3	28–57	5.0
June	15.03	19	150	50.4	28–58	4.1
July	16.30	20	172	54.9	39–66	4.5
August	16.04	21	152	56.5	45–66	1.6
September	16.61	22	—	—	—	—
October	15.34	23	198	61.4	43–72	—
November	14.82	24	156	60.9	48–72	−0.5

* 1948–49

At the estimated average of one year the mean length in a small collection was only 23.4 mm, but a large collection two months later showed a mean of 35.0 mm. At the end of the second year the mean length was 60.9 mm as compared with 42.8 mm at La Jolla. The indicated mean increase of 37.5 mm in one year makes it seem probable that the small collection at the end of the first year represented a sample of smaller sizes than the normal average at that locality (Table XIII).

At the end of the third year the mean length was 86.7 mm, indicating an increase of 25.8 mm during the year. In the fourth year an apparent gain of 17.5 mm brought the mean length to 104.2 mm (Table IX).

TABLE IX.—Rates of Growth at Point Hueneme during Third and Fourth Years

Date	*Average water* temperature*	*Average age, months*	*Number in samples*	*Length, mm*		*Indicated increase in month*
				Mean	*Range*	
December	12.95	25	—	—	—	—
January	11.10	26	270	64.4	52–78	—
February	11.43	27	49	67.3	56–77	2.9
March	12.25	28	203	67.3	55–79	0.0
April	13.05	29	35	67.4	54–79	0.1
May	14.80	30	215	71.4	58–85	4.0
June	15.03	31	154	74.8	61–89	3.4
July	16.30	32	116	78.0	66–91	3.2
August	16.04	33	114	80.4	67–95	2.4
September	16.61	34	—	—	—	—
October	15.34	35	5	85.0	77–94	—
November	14.82	36	53	86.7	73–100	1.7
December	12.95	37	—	—	—	—
January	11.10	38	33	89.6	76–111	—
February	11.43	39	11	84.9	79–97	−4.7
March	12.25	40	—	—	—	—
April	13.05	41	15	86.7	80–103	—
May	14.80	42	42	87.3	78–105	0.6
June	15.03	43	23	90.5	84–104	3.2
July	16.30	44	52	94.4	83–114	3.9
August	16.04	45	16	99.2	93–110	4.8
September	16.61	46	—	—	—	—
October	15.34	47	—	—	—	—
November	14.82	48	5	104.2	101–111	—

* 1948–49

Spawning by most individuals had been nearly completed in January. Gametogenesis in February and March was usual, although a few were apparently ripe or partially spawned out. Most individuals were apparently ripe in May. Spawning by both sexes took place in the aquarium on June 10, and the eggs produced normal larvae. All were fully ripe or partly spawned out in August.

INVESTIGATIONS AT PISMO BEACH

This beach has long been noted as one of the most productive localities on the California coast. The investigations of Weymouth (1923), Herrington (1930), Clark (1932) and Roedel (1939) were made in this area, and population studies have been continued in subsequent years by the California Bureau of Marine Fisheries.

Weymouth concluded from an examination of the growth rings that the average length of the young clams at Pismo Beach and Oceano during the first winter, when he supposed they were 4 to 6 months of age, was 22 mm and during the second winter 45 mm, but he was doubtless in error as to the ages. Our data show a mean length of 19.0 mm at the estimated age of one year and 46.7 mm at the age of two years (Tables X and XIII). This would indicate an increase of 27.7 mm during the second year. The average increment in the third year was 21.1 mm and in the fourth year 19.3 mm (Tables XI and XIII).

TABLE X.—RATES OF GROWTH AT PISMO BEACH DURING FIRST AND SECOND YEARS, INCLUDING DATA FROM WEYMOUTH (1923) AND THE CALIFORNIA STATE FISHERIES LABORATORY

Date	*Average water* temperature*	*Average age, months*	*Number in samples*	*Length, mm*		*Indicated increase in month*
				Mean	*Range*	
December	12.86	1	—	—	—	—
January	12.10	2	—	—	—	—
February	11.91	3	—	—	—	—
March	11.46	4	—	—	—	—
April	10.69	5	—	—	—	—
May	11.31	6	—	—	—	—
June	11.90	7	—	—	—	—
July	12.35	8	31	7.4	4–13	—
August	12.93	9	—	—	—	—
September	13.58	10	169	13.4	6–23	—
October	13.54	11	—	—	—	—
November	12.99	12	4232	19.0	8–36	—
December	12.86	13	44	21.2	16–25	2.2
January	12.10	14	143	27.2	12–32	6.0
February	11.91	15	231	24.5	14–36	−2.7
March	11.46	16	381	29.7	24–35	5.2
April	10.69	17	187	30.0	23–37	0.3
May	11.31	18	285	32.7	25–40	2.7
June	11.90	19	344	34.9	21–43	2.2
July	12.35	20	593	38.1	12–49	3.2
August	12.93	21	152	45.7	39–53	7.6
September	13.58	22	224	43.9	23–55	−1.8
October	13.54	23	141	49.6	42–56	5.7
November	12.99	24	2483	46.7	32–65	−2.9

* At Point Arguello

Although no data are available as to the temperature of the water directly adjacent to Pismo Beach, the mean annual temperature of the water a few miles offshore in that area averages about 13° C as compared with 16.9° at La Jolla. In October, when it is probable that the greatest number of larvae are in the water, the average temperature is only 13 to 15° and falls to 12° or lower during the winter. In some years it does not reach as high as 13° until July. At Point Arguello, only about 30 miles south of Pismo Beach, the temperature at the shore is even lower, with a yearly average of only 12.3°. The monthly average reaches as high as 13° in September and October only, while at La Jolla during these two months the average temperature of the water is 6 to 7° higher. It should be emphasized that on sunny afternoons the temperature of the water on the beach at Pismo may sometimes rise as high as 24° C and that of the sand at the level occupied by the clams may be above 21° (Weymouth, 1923).

Weymouth concluded that the spawning season at Pismo Beach

TABLE XI.—RATES OF GROWTH AT PISMO BEACH DURING THIRD AND FOURTH YEARS, INCLUDING DATA FROM WEYMOUTH (1923) AND THE CALIFORNIA STATE FISHERIES LABORATORY

Date	*Average water* temperature*	*Average age, months*	*Number in samples*	*Length, mm*		*Indicated increase in month*
				Mean	*Range*	
December	12.86	25	16	54.5	50–60	7.8
January	13.10	26	63	53.7	39–62	−0.8
February	11.91	27	264	52.3	40–66	−1.4
March	11.46	28	16	60.6	52–70	8.3
April	10.69	29	45	58.9	44–69	−1.7
May	11.31	30	106	62.8	47–70	3.9
June	11.90	31	195	62.5	45–80	−0.3
July	12.35	32	81	66.9	48–78	4.4
August	12.93	33	88	74.2	55–80	7.3
September	13.58	34	—	—	—	—
October	13.54	35	35	77.4	67–81	—
November	12.99	36	1369	67.8	64–85	−9.6
December	12.86	37	—	—	—	—
January	12.10	38	233	77.2	59–91	—
February	11.91	39	60	77.1	63–89	−0.1
March	11.46	40	—	—	—	—
April	10.69	41	136	82.0	68–98	—
May	11.31	42	323	84.2	71–96	2.2
June	11.90	43	150	90.0	77–104	5.8
July	12.35	44	175	92.2	77–107	2.2
August	12.93	45	160	91.1	80–104	−1.1
September	13.58	46	—	—	—	—
October	13.54	47	—	—	—	—
November	12.99	48	1141	87.1	—	—

* At Point Arguello

extends from July to September, although he found large eggs in some of the individuals which he examined at intervals from March to November. It has now been found, however, that while the most active spawning takes place in the summer and autumn, apparently normal ovogenesis and spermatogenesis continue in some members of the population throughout the entire year. This is not considered satisfactory proof that spawning actually takes place in midwinter and early spring, although the gonads of a small proportion of the individuals examined indicated such an occurrence. This evidence is corroborated by finding young clams only 4 mm long in July and 6 mm long in September (Table X).

The earliest observed spawning by clams from this beach occurred in the aquarium in June. But no young clams have yet been found on this beach until July of the following year. They had then attained a length of 4 to 13 mm, with a mean of 7.4 mm (Table X). Assuming a rate of increase of 1 mm a month in winter and 1.7 in the spring, it would have required about eight months to reach a length of 13 mm. Consequently, a mean of 7.4 mm in July would indicate a population averaging five to six months of age. The data for the remainder of the year are in harmony with this assumption. For these reasons it is concluded that the median date when the young have completed the larval period and settled on the beach at Pismo Beach is November, or about two months later than at La Jolla. They would then have an average age of one month in December, but presumably these dates vary considerably in different years.

The estimated sizes and ages of the clams found in equal sections of Pismo Beach by the California Bureau of Marine Fisheries in the census taken in November of each of the years 1927 to 1949, with the exception of 1942 to 1945 and 1948, are indicated in Table XII. The total of 4111 clams approximately one year of age had a mean length of 18.9 mm. Those two, three and four years old numbered 1938, 1097 and 1141 respectively, with average lengths of 44.4, 65.2 and 86.6 mm. The clams at La Jolla at the corresponding ages had average lengths of 21.5, 42.8, 62.0 and 78.9 mm. With the exception of the first group, the rates of growth were somewhat greater at Pismo Beach than at La Jolla. At Pismo Beach, moreover, the number of clams which

TABLE XII.—AVERAGE LENGTH AND YEARLY INCREMENT OF CLAMS IN THE FIRST FOUR AGE GROUPS COLLECTED AT PISMO BEACH IN NOVEMBER OF EACH YEAR BY THE CALIFORNIA BUREAU OF MARINE FISHERIES

	Av. age, 1 year		*Av. age, 2 years*			*Av. age, 3 years*			*Av. age, 4 years*		
Year	*No. in sample*	*Av. length*	*No. in sample*	*Av. length*	*Inc.*	*No. in sample*	*Av. length*	*Inc.*	*No. in sample*	*Av. length*	*Inc.*
1927	38	22.9	62	44.7	—	28	66.7	—	21	88.3	—
1928	6	22.7	32	43.1	20.2	40	61.6	16.9	23	86.5	19.8
1929	468	20.1	5	40.8	18.1	23	59.0	15.9	23	83.1	21.5
1930	357	20.1	189	43.3	23.2	5	68.2	27.4	4	84.5	25.5
1931	871	21.7	149	43.0	22.9	56	62.7	19.4	—	—	—
1932	44	21.5	279	44.5	22.8	128	63.8	20.8	103	80.8	18.1
1933	199	15.3	38	46.1	24.6	122	63.8	19.3	98	75.1	11.3
1934	0	—	70	42.6	27.3	23	69.8	23.7	80	87.6	23.8
1935	758	18.0	2	44.0	—	56	63.0	20.4	14	85.3	15.5
1936	142	21.6	270	42.6	24.6	3	63.0	19.0	45	79.2	16.2
1937	743	14.9	101	45.7	24.1	245	62.3	19.7	8	75.1	12.1
1938	9	25.6	231	38.5	23.6	90	62.4	16.7	173	82.3	20.0
1939	23	17.3	4	41.8	16.2	53	57.6	19.1	75	87.0	24.6
1940	24	21.9	34	45.2	27.8	11	70.9	29.1	19	87.1	29.5
1941	13	20.0	4	41.8	19.9	3	68.7	23.5	—	—	—
1942	—	—	—	—	—	—	—	—	—	—	—
1943	—	—	—	—	—	—	—	—	—	—	—
1944	—	—	—	—	—	—	—	—	—	—	—
1945	—	—	—	—	—	—	—	—	—	—	—
1946	384	19.4	164	49.8	—	57	73.3	—	200	92.8	—
1947	31	19.7	297	49.0	29.6	101	75.7	25.9	65	93.5	20.2
1948	—	—	—	—	—	—	—	—	—	—	—
1949	1	13.0	7	43.0	28.9	53	75.0	20.7	19	92.8	16.7
Totals	4111		1938			1097			1141		
Av. length		18.9		44.4			65.2			86.6	
Av. increase		—			25.5			20.8			21.4

were four years old was even larger than in the group one year younger, while at La Jolla relatively few individuals survive in the intertidal zone for more than three years.

Since all of the collections made by the Bureau of Marine Fisheries covered equal amounts of space in the same location on the beach in successive years, the numbers in each year-class will indicate the changes in the population from year to year. Inspection of Table XII will show that the numbers in the first year-class varied from 0 in 1934 and 1 in 1949 to 871 in 1931, the total number for the 19 years being 4111, or 50% of the total of 8287 for the four year-classes. The average lengths, omitting the single individual found in 1949, varied from 14.9 mm in 1937 to 22.9 mm in 1927 and 25.6 mm for the small number found in 1938.

The second year-class varied in number from 2 in 1935, 4 in 1939 and 1941, and 5 in 1929 to 279 in 1932 and 297 in 1947. The total number in the second year-class was 1938 or approximately 23% of the entire population of 8287 individuals not exceeding four years of age. The average lengths varied from 38.5 mm in 1938 to 49.8 mm in 1946, while the mean length at the end of the second year was 44.4 mm, indicating an average increase during the second year of 25.5 mm (Table XII).

Similarly, the third year-class varied in number from 3 in 1936 and 1941 and 5 in 1930 to 245 in 1937, the total number being 1097 or approximately 13% of the entire population not exceeding four years of age. The average lengths at the estimated average age of three years varied from 57.6 mm in 1939 to 75.7 mm in 1947, with a mean of 65.2 mm.

Of the fourth year-class, 1141 individuals were obtained. These represent about 14% of the entire collections. The numbers varied from 0 in 1931 and 4 in 1930 to 200 in 1946. The average lengths at the estimated average age of four years ranged from 75.1 mm in 1933 and 1937 to 93.5 mm in 1947, the mean length being 86.6 mm (Table XII).

These extensive collections afford excellent examples of the great variability that may be expected in dealing with populations of invertebrates, not only in the constituent year-classes, as shown in Fig. 4, but also in the rates of growth in successive years. An estimate of the rate of survival through the first four years of life may be obtained from Table XII. It is obvious that any first year-class will be followed by the second year-class in the line below, which gives the data for the following year, and so on. Hence, if the figures in Table XII be read obliquely downward and to the right they will show the fate of any first year-class in following years in so far as could be determined by the collections taken from equal areas of the beach in successive years.

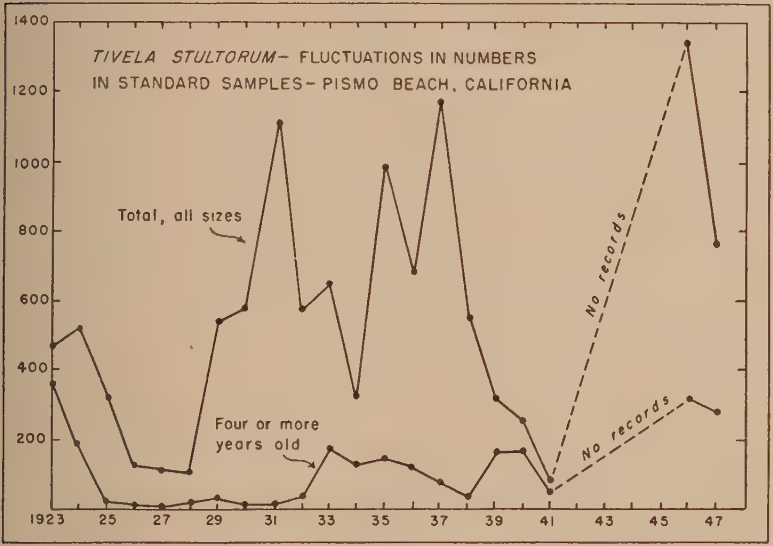

Figure 4. Fluctuations in the populations found each year in three trenches, each 16 cm. wide, in separate locations on Pismo Beach, California, at corresponding dates, 1923–1941 and 1946–47. Between 1930 and 1938 the total population showed a biennial periodicity due to an increased set of young clams in each alternate year. The relatively small number of clams reaching the age of four or more years indicates the high rate of mortality due to natural causes and human agency. (Data from Aplin, 1947 and from California State Fisheries Laboratory.)

TABLE XIII.—COMPARATIVE GROWTH RATES OF THE FIRST FOUR YEAR-CLASSES AT FIVE LOCALITIES

	Mean annual temp. of water[1]	*Average length at each age, mm*				*Average annual increment, mm*			
		1 yr.	*2 yr.*	*3 yr.*	*4 yr.*	*1 yr.*	*2 yr.*	*3 yr.*	*4 yr.*
La Jolla	16.94° C	21.5	42.8	62.0	78.9	21.5	21.3	19.2	16.9
La Jolla Shores	16.94	20.2	40.8	63.7	—	20.2	20.6	22.9	—
Sunset Beach	16.58	26.9	65.2	88.5	103.8	26.9	38.3	23.3	15.3
Hueneme	14.71	23.4	60.9	86.7	104.2	23.4	37.5	25.8	17.5
Pismo Beach	12.30	18.9	44.4	65.2	86.6	18.9	25.5	20.8	21.4

[1] At nearest temperature station, usually on a pier.

Table XIII gives a comparison of the growth rates at the five localities investigated, as indicated by the average lengths and the annual increases of the first four year-classes, including all collections. It will be noted that the most rapid growth was found at Sunset Beach, with the rate at Hueneme nearly as great and at Pismo Beach considerably less. La Jolla and La Jolla Shores, with the highest temperatures, appear to be less favorable for rapid growth and long survival than the localities with cooler water farther north or where there is extensive upwelling of cool oceanic water farther south along the Mexican Coast.

INVESTIGATIONS AT OTHER LOCALITIES

Morro Bay. The cool water at this locality is conducive to large populations of clams of legal size. In January most individuals were near the end of the spawning period or were completely spawned out, although a small percentage was continuing active gametogenesis. In February the spawned out condition predominated and in March all stages of gametogenesis were general, leading to the apparently ripe condition of some individuals in April. The first spawning observed in the aquarium was in June, although the gonads of others showed that spawning had occurred previously.

LOWER CALIFORNIA

On some of the beaches from 100 to 500 miles south of the Mexican border there is extensive upwelling of cool oceanic water and large populations of this species are produced. Collections from the following localities have been examined at intervals.

Punta Cabras (31° 20′ N. Lat.). At this locality, about 100 miles south of the Mexican border, there is extensive upwelling of cool oceanic water, with a thriving population of clams which reach a large size. All of the clams examined in February were completely spawned out and others obtained in April had only early gametogenesis. Most of those examined in May showed early gametogenesis, but some appeared fully ripe or were in postspawning condition. In September all were partly spawned out.

San Antonio del Mar (31° 06′ N. Lat.). Extensive upwelling and large populations of clams are found at this locality. Those collected in May were all nearly ripe or fully ripe and spawning took place in the aquarium. Of 36 individuals examined in July, one had recently completed spawning and all of the others appeared to be ripe. Spawning was general in the aquarium.[2]

Blanca Bay (29° 06′ N. Lat.). Here also there is cool water and an abundance of large clams. Those examined the first of April showed much variation in the condition of the gonads. Some were in the

[2] Most of the population at this locality died in the early autumn of 1950. The cause has not yet been determined.

early stages of gametogenesis, while others were nearly ripe, fully ripe or partly spawned out. In July all were ripe or partly spawned out.

Thurloe Bay (27° 38′ N. Lat.). Although more than 450 miles south of the Mexican border, the water is cool and conditions are suitable for the production of clams of large size. All of the individuals examined in January were in various stages of gametogenesis but not ripe. Some of those examined in early April were fully ripe or partially spawned, while others were recently spawned out. In July also some were ripe, some were spawned out and others half ripe. It is concluded that the spawning season at favorable localities on the Mexican coast is even less definitely seasonal than it is on the coast of California.

SUMMARY

The fluctuations of the populations have been studied by collecting large samples and returning them to the beach after measurement at monthly intervals for five successive years at La Jolla, California and for two to three years at three other widely separated localities. Many marked individuals were also replanted on the beach and remeasured monthly.

The area investigated at La Jolla covered about 2000 square meters of a beach legally protected from human interference. The constituent year-classes in the population varied considerably from year to year due to differences in the initial set of young clams and the subsequent mortality. It is estimated that an average of three young clams arrived on each square meter each year, but the annual mortality has been from 67 to 75% for each year-class. Of the average annual set of approximately 6000, only about 2000, 700, 170 and 50, respectively, have remained at the end of the first to fourth years. Less than one per cent of the population survived for four years and clams of the legal length of 127 mm were usually found only in deeper, cooler water.

At the other localities investigated, Sunset Beach, Hueneme and Pismo Beach, conditions are more favorable, growth is more rapid and large crops of legal size are produced annually. Many individuals reach an age of seven to twelve years or more. Nevertheless, the mortality rate for each year-class at Pismo Beach, in part due to human agencies, has been estimated as 55, 45, 29, 34, 52, 68 and 72%, respectively, from the first to seventh years.

The populations at Pismo Beach enumerated by the California Bureau of Marine Fisheries in November of 19 years between 1927 and 1949 indicated that an average of 50% of those not more than four years of age belonged to the first year-class and 23, 13 and 14%, respectively, to the second, third and fourth year-classes. Wide fluctuations were found. In some years only 0 to 10% of the population belonged to the first year-class, while in other years this year-class comprised 60 to 80% of the population.

The most productive areas, both on the Californian and Mexican coasts, are generally those with extensive upwelling of cool oceanic water, bringing with it the inorganic nutrients essential for the growth of the phytoplankton and indirectly for the other organisms and detritus on which the nutrition of the clam depends.

The annual increment in length averages 21 to 25 mm the first and second years of life and somewhat less thereafter. The length of 127 mm, which is the minimum legal size, is reached in five to eight years. The principal spawning season is June to December, although a small proportion of the population has apparently ripe sexual products at any season of the year.

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[2] See for additional references.

NOTE ON THE DYNAMICS OF THE GULF STREAM[1]

By

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ABSTRACT

The nonlinear inertial terms have been neglected in Stommel's and in Munk's theory for the wind-driven ocean circulation. Using a method of successive approximations, the effect of these terms on the mass transport in the Gulf Stream region has been computed under greatly simplifying assumptions. These assumptions involve Reid's model of the vertical density structure, which consists of an exponential decrease in the density upward to the thermocline and a homogeneous upper layer. Assuming first a constant depth of thermocline and a north-south boundary, the principal modification is a displacement downstream by about 7° latitude of the region of maximum currents. The displacement is smaller in the case of a coastline whose orientation deviates from a north-south direction. Assuming next a variation in the depth of thermocline across the stream, this asymmetry of the mass transport circulation relative to the wind circulation is reduced. It is also shown that the density model specifies a relation between the vertically integrated transport and the surface transport, according to which the width of the "cold wall" at the surface is only 40% of that of the integrated transport. Two observed features which could not be accounted for by the linear theory, the countercurrent inshore and the continued sharpness of the Gulf Stream's western boundary long after it has left the American east coast, are apparently not contained in the higher order solutions.

INTRODUCTION

The narrow fast currents that flow along the western boundaries of the oceans are among the most striking oceanographic phenomena. The outstanding examples are the Kuroshio current off the coast of Japan and the Gulf Stream system off the American east coast. During the last few years Iselin and Fuglister (1948) and Von Arx (1950) have made detailed surveys of the Gulf Stream with new instruments and techniques, among them continuous temperature and current recorders and radio aids to navigation. These measurements have only served to emphasize the great speed of the Gulf Stream and the sharpness of its western boundary. This sharp definition of the current, which prompted Benjamin Franklin to call it a great river in

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[1] Contribution from the Scripps Institution of Oceanography, New Series No. 496. This work represents research carried out for the Office of Naval Research, Navy Department.

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the sea, is perhaps its most striking characteristic. Any adequate theory, and there have been many, must account for it.

Unfortunately there are two theories, both of which explain, though for different reasons, the existence of such intense and well defined currents. The earlier one is Rossby's (1936) "wake stream" or "jet stream" theory, which represents one of his several remarkable attempts to adapt results in fluid mechanics to meteorology and physical oceanography. The Gulf Stream is interpreted as "a current moving under its own momentum and produced by discharging water into the basin through a 'jet'" (the Straits of Florida). The other theory is that of Stommel (1948), which explains the westward intensification of ocean currents as the result of the earth's rotation on the wind-driven ocean circulation. The theory has been extended by Munk (1950), and for reasons discussed in Munk's paper it will be referred to as the "planetary vorticity" theory.

Both theories have attractive features. The wake stream theory accounts for the increase downstream in width and mass transport of the Gulf Stream as well as a countercurrent on the inshore side of the Gulf Stream.[5] The planetary vorticity theory leads to the right order of magnitude for the mass transport of the Gulf Stream, and it accounts for a countercurrent on the offshore side. One is therefore tempted to combine the two theories into a unified dynamic picture of the Gulf Stream.

The fundamental difference appears to be that in Stommel's and in Munk's linear theory the inertial terms in the equations of motion have been neglected whereas in Rossby's theory these terms play a predominant role. Munk estimates the magnitude of these terms *a posteriori* and finds them to be small "except along the inshore edge of the western current," where he expects his conclusions to be modified in the sense prescribed by Rossby. The procedure here will be to consider Munk's solution to the linear theory as a zero approximation and to introduce the inertial terms into the first and second order approximations.

The mathematics soon becomes so involved that we have found it essential to check each step by independent calculations. Only the outline of the procedure is sketched here. We suggest that the reader confine his attention to the discussion of the somewhat meager results from our tedious calculations.

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[5] The first mention of a countercurrent in the slope water was made in 1590 by John White, who remarked that in order to stay within the Gulf Stream one had to stand far out to sea, because along the coast there were "eddy currents setting to the south and southwest."

THE EQUATIONS OF MOTION

The notation follows Munk (1950); equations from this paper will be referred to by the letter A. The inertial terms appear on the left sides of equations A1, A4, A6 in the following forms:[6]

$$\rho\mathbf{v}\cdot\nabla\mathbf{v}\,, \quad \int_{-\infty}^{h}\rho\mathbf{v}\cdot\nabla\mathbf{v}dz\,, \quad -\nabla\times\int_{-\infty}^{h}\rho\mathbf{v}\cdot\nabla\mathbf{v}dz\,.$$

In the linear theory it was found possible to write all equations in terms of vertically integrated functions without having to specify the manner in which density varies with depth. This is no longer possible if the quadratic terms are to be considered.

Reid (1948) has introduced a simple model for the density distribution. Let the z-axis be directed upwards from a level surface just beneath the sea surface, and let h designate the elevation of the sea surface and H the distance beneath the level reference surface to which a homogeneous upper layer of density ρ_0 extends. Beneath the homogeneous layer, Reid assumes an exponential distribution

$$\rho = \rho_\infty - \Delta\rho e^{1+z/H},$$

where $\Delta\rho = \rho_\infty - \rho_0$, and ρ_∞ is the density at great depth ($z = -\infty$).

The horizontal pressure gradient vanishes at great depth, i. e. $\int_{-\infty}^{h}\rho\,dz =$ constant, which yields

$$\frac{h}{H} = \frac{2\Delta\rho}{\rho_0}\,, \tag{1}$$

provided the reference level is properly selected.

The pressure gradient in the x-direction is then given for the upper layer by

$$\frac{\partial p_0}{\partial x} = g\rho_0\frac{\partial h}{\partial x} \tag{2}$$

and for the lower layer by

$$\frac{\partial p}{\partial x} = \frac{1}{2}\,g\rho_0 e^{1+z/H}\,(1 - z/H)\,\frac{\partial h}{\partial x}\,, \tag{3}$$

where use has been made of (1). Similar expressions are valid for $\partial p/\partial y$. According to the geostrophic law, the pressure gradients are proportional to the horizontal velocity components. If $\mathbf{v}_0$ denotes the velocity vector in the upper layer, then

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[6] Here h and $-\infty$ replace z_0 and $-h$, respectively, in the original notation, without any essential change in meaning.

$$\frac{1}{2}\,\mathbf{v}_0\,e^{1+z/H}(1 - z/H)$$

is the corresponding velocity at depths beneath the homogeneous layer. It follows that

$$\int_{-\infty}^{h} \bar{\rho}\mathbf{v} \cdot \nabla\mathbf{v}dz = \frac{29}{16}\,\bar{\rho}H\,(\mathbf{v}_0 \cdot \nabla)\,\mathbf{v}_0 + \frac{29}{32}\,\bar{\rho}\mathbf{v}_0\,(\mathbf{v}_0 \cdot \nabla)\,H\,.$$

The second term is negligible since H is nearly constant along a stream line. The first term can be combined with

$$\boldsymbol{M} \equiv \int_{-\infty}^{h} \rho\mathbf{v}dz = \frac{5}{2}\,\bar{\rho}H\mathbf{v}_0 \tag{4}$$

to yield

$$\int_{-\infty}^{h} \bar{\rho}\mathbf{v}\cdot\nabla\mathbf{v}dz = c\boldsymbol{M}\cdot\nabla\boldsymbol{M}\,, \tag{5}$$

where

$$c = 29/100\bar{\rho}H\,, \tag{6}$$

provided variations in density are small compared to the mean density $\bar{\rho}$.

The equation of mass transport A6 then becomes

$$\left(A\nabla^4 - \beta\,\frac{\partial}{\partial x}\right)\psi + \mathrm{curl}_z\,\boldsymbol{\tau} = c\,\mathrm{curl}_z\,(\boldsymbol{M} \cdot \nabla\boldsymbol{M}) = c\,(\boldsymbol{M} \cdot \nabla)\,\nabla^2\psi\,, \tag{7}$$

where

$$\boldsymbol{M} = \boldsymbol{k} \times \nabla\psi$$

and curl_z designates the vertical component of the vector operator. The term on the right side of equation (7) is essentially the advection of vorticity and represents the inertial effect.

For a wind system we set

$$\tau_x = -\,\Gamma\cos ny\,, \quad \tau_y = 0\,,$$

giving maximum easterlies at $y = 0$ and maximum westerlies at $y = \pi/n$.

THE CASE OF NORTH-SOUTH BOUNDARIES AND CONSTANT DEPTH OF THERMOCLINE

For this case c is a constant. It is convenient to adopt the following nondimensional co-ordinate system:

$$\begin{aligned} x' &= kx & \psi' &= \frac{\beta}{\Gamma n r}\,\psi \\ y' &= ky & & \\ r' &= kr & \boldsymbol{M}' &= \frac{\beta}{k\Gamma n r}\,\boldsymbol{M} \\ y'' &= ny & \lambda &= \frac{n^4 r \Gamma c}{4\beta^2\gamma^7}\,, \end{aligned} \tag{8}$$

where

$$k^3 = \beta/A\,, \quad \gamma = n/k\,. \tag{9}$$

It follows that

$$\frac{\partial}{\partial x} = k\,\frac{\partial}{\partial x'}\,, \qquad \frac{\partial}{\partial y} = k\,\frac{\partial}{\partial y'}\,, \qquad \nabla^4 = k^4 \nabla'^4\,, \tag{10}$$

so that the differential equation becomes

$$\left(\nabla'^4 - \frac{\partial}{\partial x'}\right)\psi' = \frac{1}{r'}\sin y'' + 4\gamma^{-1}\lambda\,\mathrm{curl}_z\,(\boldsymbol{M}'\cdot\nabla'\boldsymbol{M}')\,, \tag{11}$$

$$\boldsymbol{M}' = \boldsymbol{k}\times\nabla'\psi'\,. \tag{12}$$

The boundary conditions are

$$\psi' = 0\,, \qquad \frac{\partial\psi}{\partial x'} = 0\,, \tag{13}$$

at the western boundary ($x' = 0$) and eastern boundary ($x' = r'$); the latter can be replaced by $x' = \infty$ as long as we confine our attention to conditions near the western boundary.

Successive Approximations. The first term on the right-hand side of equation (11) represents the driving force of the wind, the second term incorporates the effect of the neglected inertial terms. The relative importance of these inertial terms depends on the value of λ, and it seems reasonable to expand the solution in the following power series:

$$\psi' = \psi_0' + \lambda\psi_1' + \lambda^2\psi_2' + \ldots \tag{14}$$

We shall show later that the value of λ is about 0.3 so that the series converges fairly rapidly. Substituting (14) into equations (11) and (12) and equating equal powers of λ gives

$$\left(\nabla'^4 - \frac{\partial}{\partial x'}\right)\psi_0' = \frac{1}{r'}\sin y''\,, \tag{11.0}$$

$$\left(\nabla'^4 - \frac{\partial}{\partial x'}\right)\psi_1' = 4\gamma^{-1}\,\mathrm{curl}_z\,(\boldsymbol{M}_0'\cdot\nabla'\boldsymbol{M}_0')\,, \tag{11.1}$$

$$\left(\nabla'^4 - \frac{\partial}{\partial x'}\right)\psi_2' = 4\gamma^{-1}\,\mathrm{curl}_z\,(\boldsymbol{M}_0' \cdot \nabla'\boldsymbol{M}_1' + \boldsymbol{M}_1' \cdot \nabla'\boldsymbol{M}_0')\,, \tag{11.2}$$

and so forth. Equation (12) holds for each order, that is,

$$\boldsymbol{M}_i' = \boldsymbol{k} \times \nabla'\psi_i' \qquad i = 0, 1, 2, \ldots \tag{12i}$$

The Zero Order. To the zero approximation the inertial terms are neglected and the solution to (11.0) becomes (Munk and Carrier, 1950)

$$\psi_0' = X_0 \sin y'', \tag{15.0}$$

where

$$X_0 = 1 + \frac{i\sqrt{3}\omega}{3}e^{\omega^2 x'} - \frac{i\sqrt{3}\omega^2}{3}e^{\omega x'} - \frac{x'}{r'}, \tag{16.0}$$

and

$$\omega = -\frac{1}{2} + \frac{i\sqrt{3}}{2}, \qquad \omega^2 = -\frac{1}{2} - \frac{i\sqrt{3}}{2}, \qquad \omega^3 = 1$$

are the cube roots of one. The last term in (16.0) plays a negligible role in the western boundary zone of a wide ocean.

The First Order. The computation is very cumbersome and hence only the major steps will be outlined here. The right side of equation (11.1) is now a known function of x', since it can be found from equations (15.0) and (16.0). It reduces to the form

$$2F_1 \sin 2y'', \tag{17.1}$$

where

$$F_1 = \frac{\partial X_0}{\partial x'}\,\frac{\partial^2 X_0}{\partial x'^2} - X_0\frac{\partial^3 X_0}{\partial x'^3} \tag{18.1}$$

$$= -\,e^{-x'} - \frac{i\sqrt{3}\omega}{3}e^{\omega^2 x'} + \frac{i\sqrt{3}\omega^2}{3}e^{\omega x'}. \tag{19.1}$$

The particular and homogeneous integrals of (11.1) are respectively

$$\psi_1'^p = \left[-e^{-x'} - \frac{2i\sqrt{3}\omega}{9}x'e^{\omega^2 x'} + \frac{2i\sqrt{3}\omega^2}{9}x'e^{\omega x'}\right]\sin 2y''\,, \tag{20.1}$$

$$\psi_1'^h = [a_1 e^{\omega^2 x'} + \bar{a}_1 e^{\omega x'}]\sin 2y''. \tag{21.1}$$

The constants a_1 and $\bar{a}_1$ are determined by subjecting the complete solution $\psi_1' = \psi_1'^p + \psi_1'^h$ to the boundary conditions (13):

$$a_1 = \frac{1}{2} - \frac{7i\sqrt{3}}{18}, \qquad \bar{a}_1 = \frac{1}{2} + \frac{7i\sqrt{3}}{18}. \tag{22.1}$$

The solution is

$$\psi_1' = X_1 \sin 2y'', \tag{23.1}$$

$$X_1 = -\,e^{-x'} + (m_1 + in_1)e^{\omega^2 x'} + (m_1 - in_1)e^{\omega x'}, \tag{24.1}$$

where

$$m_1 = \frac{1}{2} + \frac{1}{3}\,x', \qquad n_1 = -\,\frac{7\sqrt{3}}{18} + \frac{\sqrt{3}}{9}\,x'.$$

The Second Order. Substituting the first order solution (23.1) into the right side of the second order equation (11.2) gives

$$(2F_2 - 4G_2)\sin y'' + (2F_2 + 4G_2)\sin 3y'', \tag{17.2}$$

where

$$F_2 = \frac{\partial^2 X_0}{\partial x'^2}\,\frac{\partial X_1}{\partial x'} - X_0\,\frac{\partial^3 X_1}{\partial x'^3} \tag{18.2a}$$

$$\left.\begin{aligned} &= \left(\frac{2}{3}\,x' - \frac{19}{9}\right)e^{-x'} - (m_2 - in_2)e^{\omega^2 x'} - (m_2 + in_2)e^{\omega x'} \\ &\qquad - \frac{4}{9}\,e^{2\omega^2 x'} - \frac{4}{9}\,e^{2\omega x'} + e^{(\omega^2-1)x'} + e^{(\omega-1)x'}\,; \end{aligned}\right\} \tag{19.2a}$$

$$G_2 = \frac{\partial X_0}{\partial x'}\,\frac{\partial^2 X_1}{\partial x'^2} - \frac{\partial^3 X_0}{\partial x'^2}\,X_1 \tag{18.2b}$$

$$\left.\begin{aligned} &= \left(\frac{2}{3}\,x' + \frac{1}{9}\right)e^{-x'} + \frac{4}{9}\,e^{2\omega^2 x'} + \frac{4}{9}\,e^{2\omega x'} \\ &\qquad + \omega^2 e^{(\omega2-1)\,x'} + \omega e^{(\omega-1)x'}\,; \end{aligned}\right\} \tag{19.2b}$$

and

$$m_2 = -\,\frac{1}{2} + \frac{x'}{3}, \qquad n_2 = \frac{\sqrt{3}}{18} - \frac{\sqrt{3}x'}{9}.$$

The particular integral equals

$$\left.\begin{aligned} \psi_2'^{p} = &\left\{\left(-\frac{2}{3}\,x' - 4\right)e^{-x'} + (m' + in')\,e^{\omega^2 x'} + (m' - in')\,e^{\omega x'}\right. \\ &\quad - \frac{4\omega}{21}\,e^{2\omega^2 x'} - \frac{4\omega^2}{21}\,e^{2\omega x'} + \frac{1}{21}\,(13\omega^2 + 11)\,e^{(\omega2-1)x'} \\ &\quad \left. + \frac{1}{21}\,(13\omega + 11)\,e^{(\omega-1)x'}\right\}\sin y'' + \left\{\left(2x' + \frac{28}{9}\right)e^{-x'}\right. \\ &+ (m' + in')\,e^{\omega^2 x'} + (m' - in')\,e^{\omega x'} + \frac{4\omega}{63}\,e^{2\omega^2 x'} + \frac{4\omega^2}{63}\,e^{2\omega x'} \\ &\quad \left. + \frac{1}{7}\,(\omega - 2)\,e^{(\omega2-1)x'} + \frac{1}{7}\,(\omega^2 - 2)\,e^{(\omega-1)x'}\right\}\sin 3y'', \end{aligned}\right\} \tag{20.2}$$

where

$$m' = -\frac{1}{9}x'^2 - \frac{1}{9}x', \qquad n' = -\frac{\sqrt{3}}{27}x'^2 + \frac{5\sqrt{3}}{27}x'.$$

The homogeneous solution is

$$\psi_2'^h = [a_2 e^{\omega^2 x'} + \bar{a}_2 e^{\omega x'}] \sin y'' + [b_2 e^{\omega^2 x'} + \bar{b}_2 e^{\omega x'}] \sin 3y'', \quad (21.2)$$

where, according to the boundary conditions,

$$a_2 = \frac{71}{42} + \frac{115i\sqrt{3}}{378}, \qquad b_2 = -\frac{7}{6} - \frac{173i\sqrt{3}}{378},$$

and $\bar{a}_2$, $\bar{b}_2$ are the corresponding conjugates. The complete second order solution is found by adding $\psi_2'^p$ to $\psi_2'^h$.

THE CASE OF THE INCLINED BOUNDARY

Munk and Carrier (1950) have treated the case of a triangular ocean, with a western boundary inclined by an angle θ from a north-south direction. For an application of the foregoing results to the Gulf Stream, whose over-all direction along the western boundary of the Atlantic is more nearly eastward than northward, it is necessary to see what modifications are introduced by such an inclination.

It will be convenient to introduce the parameter

$$p^3 = \cos^4\theta \quad (25)$$

and to transform to the co-ordinate system

$$\xi = px' - py'\tan\theta, \qquad \zeta = y'. \quad (26)$$

Here ξ represents the (nondimensional) distance from the inclined western boundary. Then

$$\begin{aligned} \frac{\partial}{\partial x'} &= p\frac{\partial}{\partial \xi}, & \frac{\partial}{\partial y'} &= -p\tan\theta\frac{\partial}{\partial \xi}, \\ \nabla' &= \boldsymbol{q}\frac{\partial}{\partial s} + \boldsymbol{j}\frac{\partial}{\partial \zeta}, & \nabla'^4 &= p\frac{\partial^4}{\partial \xi^4}, \end{aligned} \quad (27)$$

where $\boldsymbol{q} = p(\boldsymbol{i} - \boldsymbol{j}\tan\theta)$. The approximations involved are discussed in Munk and Carrier (1950). It follows that

$$\mathrm{curl}_z\,(\boldsymbol{M}' \cdot \nabla'\,\boldsymbol{M}') = p^{3/2}\,(\psi_\xi'\psi_{\xi\xi\zeta}' - \psi_\zeta'\,\psi_{\xi\xi\xi}'),$$

whereas previously

$$\mathrm{curl}_z\,(\boldsymbol{M}' \cdot \nabla'\,\boldsymbol{M}') = \psi_{x'}'\,\psi_{x'x'y'}' - \psi_{y'}'\,\psi_{x'x'x'}'.$$

Making the appropriate substitutions, the differential equation (11) becomes

$$\left(\nabla'^4 - \frac{\partial}{\partial\xi}\right)\psi' = \frac{1}{pr'}\sin y'' + 4\gamma^{-1}\sqrt{p}\,\lambda\,\mathrm{curl}_z\,(\boldsymbol{M}'\cdot\nabla'\boldsymbol{M}')\,, \quad (28)$$

with the understanding that all operations now involve ordinary Cartesian operators with respect to ξ and ζ, and not those defined in (27). Thus in equation (28)

$$\nabla'^4 = \frac{\partial^4}{\partial\xi^4} + 2\frac{\partial^4}{\partial\xi^2\partial\zeta^2} + \frac{\partial^4}{\partial\zeta^4}\,, \qquad \boldsymbol{M}' = \boldsymbol{k}\times\left(\boldsymbol{i}\frac{\partial\psi'}{\partial\xi} + \boldsymbol{j}\frac{\partial\psi'}{\partial\zeta}\right),$$

etc. Equations (28) and (11) are equivalent and the previously derived solutions apply, provided we write

$$\begin{array}{llll} & \sqrt{p}\,\lambda\,, & pr'\,, & \xi \\ \text{for} & & & \\ & \lambda\,, & r'\,, & x'\,. \end{array} \quad (29)$$

For $\theta = 0$, $p = 1$, the solution reduces again to the case of north-south boundary.

DISCUSSION OF SOLUTION

The solution in real form for the north-south boundaries is then

$$\psi' = X_0 \sin y'' + \lambda X_1 \sin 2y'' + \lambda^2 (X_2{}^a \sin y'' + X_2{}^b \sin 3y'') + \ldots \quad (22)$$

where

$$X_0 = 1 - \left[\cos\frac{\sqrt{3}}{2}x' + \frac{\sqrt{3}}{3}\sin\frac{\sqrt{3}}{2}x'\right]e^{-\frac{1}{2}x'}\,, \quad (23.0)$$

$$X_1 = \left[\left(1 + \frac{2}{3}x'\right)\cos\frac{\sqrt{3}}{2}x' + \left(-\frac{7\sqrt{3}}{9} + \frac{2\sqrt{3}}{9}x'\right)\sin\frac{\sqrt{3}}{2}x'\right]e^{-\frac{1}{2}x'} - e^{-x'}\,, \quad (23.1)$$

$$\begin{aligned} X_2{}^a = {} & \left[\left(-\frac{2}{9}x'^2 - \frac{2}{9}x' + \frac{71}{21}\right)\cos\frac{\sqrt{3}}{2}x' + \left(-\frac{2\sqrt{3}}{27}x'^2 + \frac{10\sqrt{3}}{27}\right.\right. \\ & \left.\left. + \frac{115\sqrt{3}}{189}\right)\sin\frac{\sqrt{3}}{2}x'\right]e^{-\frac{1}{2}x'} + \left[\frac{4}{21}\cos\sqrt{3}x' - \frac{4\sqrt{3}}{21}\sin\sqrt{3}x'\right. \\ & \left. - \frac{2}{3}x' - 4\right]e^{-x'} + \left[\frac{3}{7}\cos\frac{\sqrt{3}}{2}x' - \frac{13\sqrt{3}}{21}\sin\frac{\sqrt{3}}{2}x'\right]e^{-\frac{3}{2}x'} \end{aligned} \quad (23.2a)$$

$$
\begin{aligned}
X_2{}^b = \Bigg[\Bigg(&-\frac{2}{9}x'^2 - \frac{2}{9}x' - \frac{7}{3}\Bigg)\cos\frac{\sqrt{3}}{2}x' + \Bigg(-\frac{2\sqrt{3}}{27}x'^2 \\
&+ \frac{10\sqrt{3}}{27}x' - \frac{173\sqrt{3}}{189}\Bigg)\sin\frac{\sqrt{3}}{2}x'\Bigg]e^{-\frac{1}{2}x'} + \Bigg[-\frac{4}{63}\cos\sqrt{3}\,x' \\
&+ \frac{4\sqrt{3}}{63}\sin\sqrt{3}x' + 2x' + \frac{28}{9}\Bigg]e^{-x'} + \Bigg[-\frac{5}{7}\cos\frac{\sqrt{3}}{2}x' \\
&\qquad + \frac{\sqrt{3}}{7}\sin\frac{\sqrt{3}}{2}x'\Bigg]e^{-\frac{3}{2}x'}\ . \qquad (23.2b)
\end{aligned}
$$

We shall first discuss this solution and then point out the modifications introduced by an inclination of the boundary relative to the north-south direction.

The four functions X of the zero, first and second order approximations are plotted in Fig. 1. The streamlines of the zero, first and second order solution are plotted separately in Fig. 2. The three parts of the figure must be combined, each part being weighted according to the value of λ. We shall leave aside for the present the question of the value of λ and consider separately the patterns corresponding to the various orders. Allowance must be made for the exaggeration of the west-east scale relative to the north-south scale by a factor of $10\pi/96\gamma$, or about 8. Thus the north-flowing currents are much more intense than they appear on the figures.

The left part of Fig. 2 gives essentially the solution discussed in Munk (1950). The first order solution (Fig. 2, center) reveals four vortices with a saddle point at their center. The eastern vortex pair is of relatively small interest, as the neglect of the last term in equation (16.0) introduces errors in the Sargasso Sea area. Of the western vortex pair, the southern vortex weakens the Gulf Stream near shore, the northern vortex strengthens it. The second order solution (Fig. 2, right) reveals three vortices.

The net modification introduced by the first and second order terms can be seen qualitatively to consist of strengthening the current in northern latitudes where all of the terms add and of weakening the current in the central portion. As a result the circulation pattern is displaced northward. This result could have been anticipated, as one would naturally expect the effect of inertia to reduce the current strength in a region of acceleration and to increase it in a region of deceleration.[7]

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[7] More precisely, to diminish vorticity in regions where the vorticity increases downstream, and vice versa.

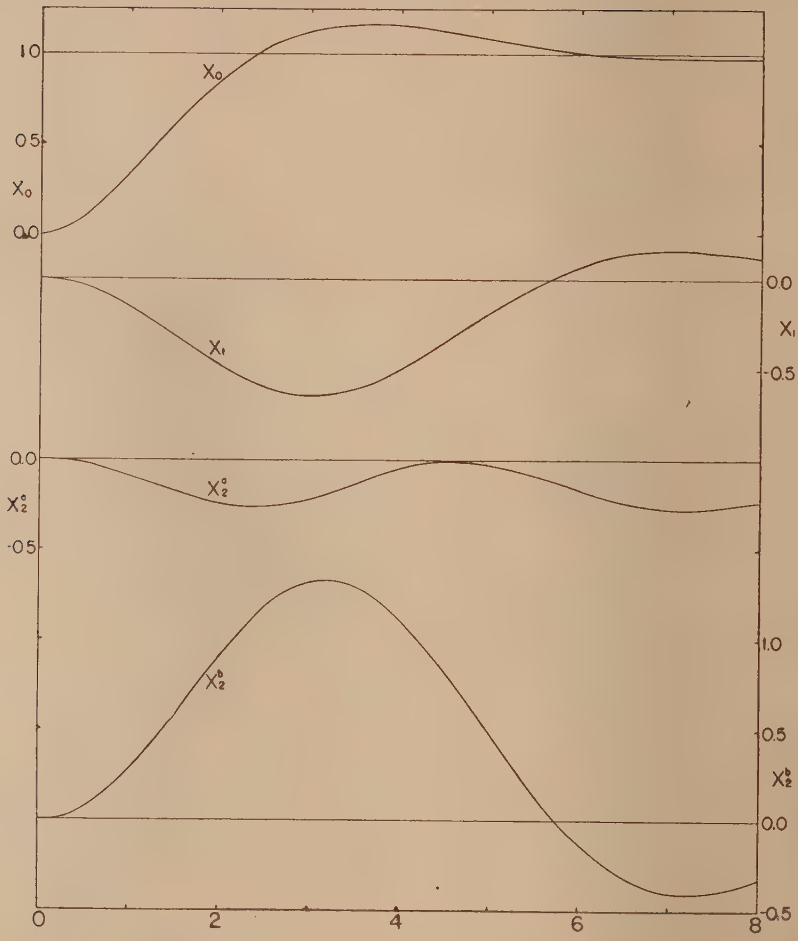

Figure 1. The finctions X of the zero, first and second orders, plotted against the non-dimensional distance x' from the western boundary.

The quantitative extent of these modifications depends upon the numerical value of λ. Setting $\pi/n = 35°$ latitude, $r'' = 6$, $\Gamma = 0.65$ dynes cm^{-2}, $\beta = 2 \times 10^{-13}$ cm^{-1} sec^{-1}, $\gamma = 0.04$, $\bar{\rho} = 1.025$ g cm^{-3} gives [equations (6) and (8)]

$$\lambda = 2784/H\,, \tag{30}$$

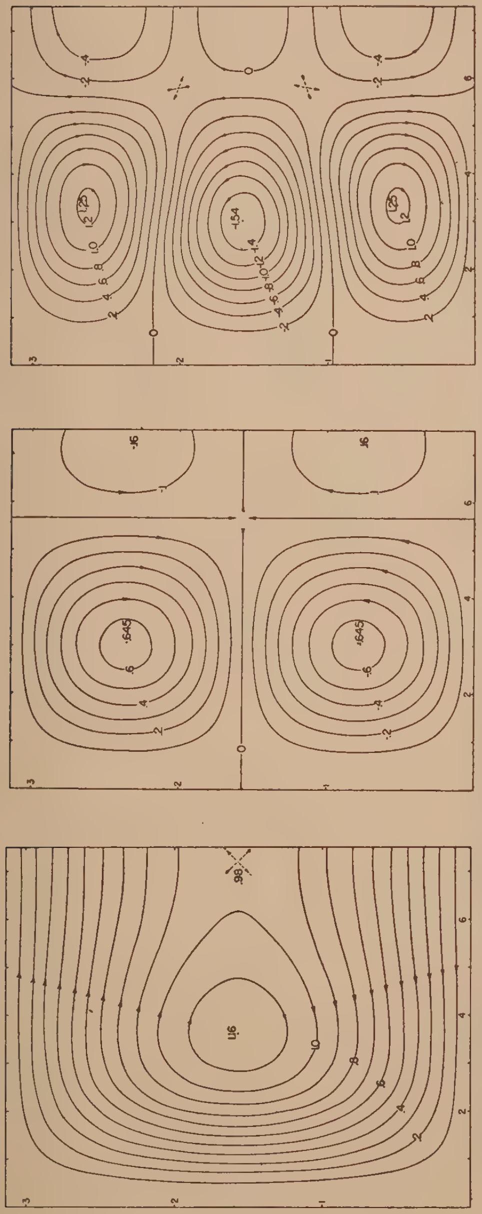

Figure 2. Streamlines of mass transport. The nondimensional west-east scale is exaggerated relative to the north-south scale by a factor of about 8, so that the currents are much more intense than they appear in the figure. *Left*: zero order solution ψ_0'; center: first order solution ψ_1'; right: second order solution ψ_2'.

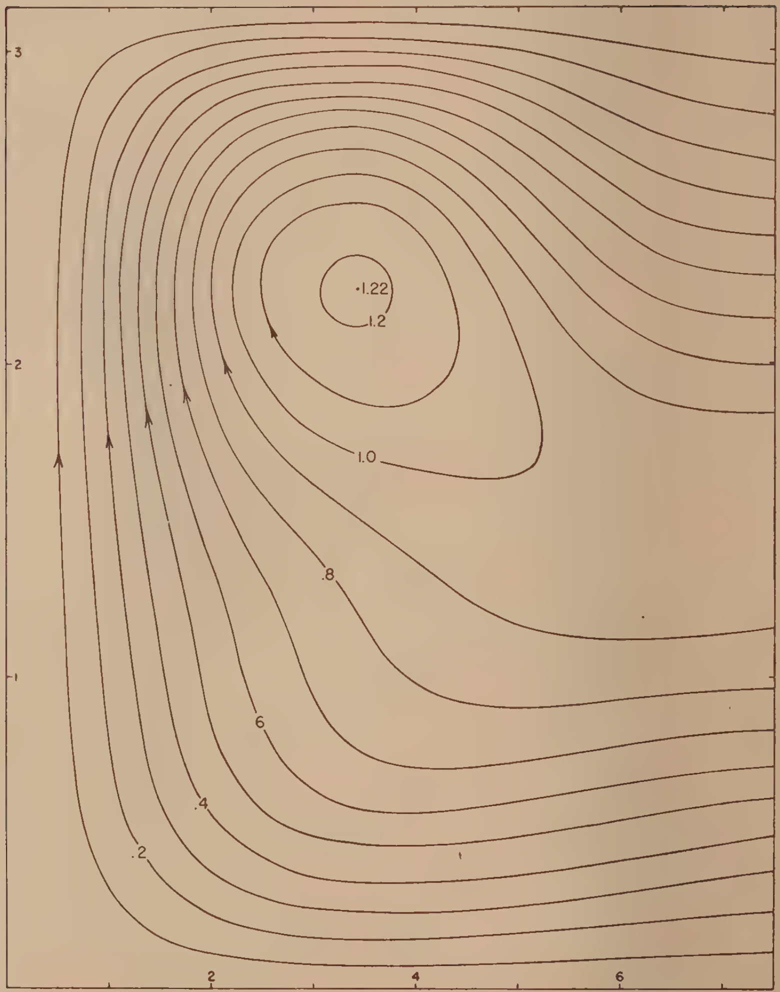

Figure 3. Streamlines of mass transport, ψ', for the sum of the zero, first, and second order solutions, assuming $\lambda = 0.4$.

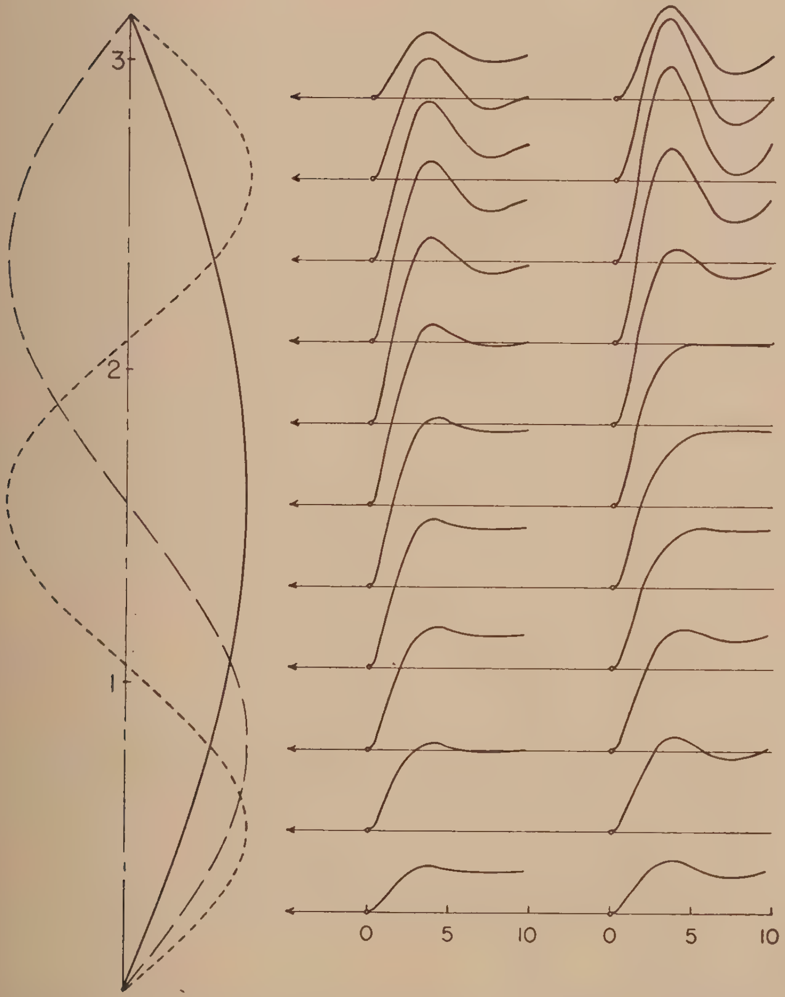

Figure 4. Profiles across Gulf Stream at various latitudes. The curves to the left represent $\sin y''$, $\sin 2y''$, and $\sin 3y''$ as functions of y'', from $y'' = 0$ (15° N) to $y'' = \pi$ (50° N). The two columns to the right represent ψ' as function of x' at the latitudes indicated by the arrows, for $\lambda = 0.2$ (left) and $\lambda = 0.4$ (right). Unit values of ψ' correspond to twice the vertical distance between arrows.

where H is the thermocline depth in cm. Assuming a thermocline depth of 70 meters gives roughly $\lambda = 0.4$. Fig. 3 has been drawn for this value. The main current reaches its greatest intensity along $y'' = 0.7\pi$ instead of $y'' = 0.5\pi$. This represents a displacement northward by 7° latitude. Fig. 4 shows the combined profiles at various latitudes, for $\lambda = 0.2$ and $\lambda = 0.4$.

The general orientation of the Atlantic coastline differs markedly from the assumed north-south direction. The effect of the inclination of the coastline is to distort the circulation pattern and widen and weaken the current by a factor $(\sec\theta)^{1/3}$, as had already been pointed out by Munk and Carrier (1950). The relative effect of the higher order terms diminishes with the inclination of the coastline (equation 29), since the value of λ is to be multiplied by $\sqrt{p}$ or $(\cos\theta)^{2/3}$. For $\theta = 50°$, this amounts to 0.74.

THE CASE OF A VARIABLE THERMOCLINE DEPTH

We have assumed λ, and hence the depth of the thermocline, to be constant. Actually λ is considerably larger near shore, where the thermocline is shallow, than it is further offshore. This variation of thermocline depth *across* the current forms a vital part in Rossby's discussion.

To estimate the importance of this variation, set

$$H = \frac{H_0}{1 - \alpha\psi'}, \qquad \lambda_0 = \frac{29 n^4 r \Gamma c}{400 \bar{\rho} \beta^2 \gamma^2 H_0}, \tag{31}$$

where H_0 is now the thermocline depth at the boundary. H will thus increase with distance from shore, reaching a value $H_0/(1 - \alpha)$ where ψ' becomes unity (Fig. 7).

Combining (31) with (6) and (8) gives

$$\left(\nabla'^4 - \frac{\partial}{\partial x'}\right)\psi' = \frac{1}{r'}\sin y'' + 4\gamma^{-1}\lambda_0(1 - \alpha\psi')\,\mathrm{curl}_z\,(\boldsymbol{M}' \cdot \nabla'\boldsymbol{M}') \tag{11v}$$

in place of equation (11). Carrying out solutions of this equation to only zero and first orders leads to equation (11.0) as before, and adds a new term

$$-\,2\alpha X_0 \mathrm{F}_1 \sin y'' \sin 2y''$$

to equation (11.1). The particular and homogeneous integrals corresponding to $X_0 F_1 \sin y'' \sin 2y''$ are

$$\left.\begin{aligned}\psi_v'^{p} = \Bigg[-\frac{5}{6}e^{-x'} - \frac{i\sqrt{3}\omega}{9}x'e^{\omega^2 x'} + \frac{i\sqrt{3}\omega^2}{9}x'e^{\omega x'} + \frac{1}{42}e^{2\omega^2 x'} \\ + \frac{1}{42}e^{2\omega x'} - \frac{i\sqrt{3}}{126}(5+\omega)\, e^{(\omega^2-1)x'} \\ + \frac{i\sqrt{3}}{126}(5+\omega^2)\, e^{(\omega-1)x'}\Bigg] \sin y'' \sin 2y'' ,\end{aligned}\right\} \qquad (20v)$$

$$\psi_v'^{h} = [a_v e^{\omega 2x'} + \bar{a}_v e^{\omega x'}] \sin y'' \sin 2y'' , \qquad (21v)$$

where

$$a_v = \frac{8}{21} - \frac{25i\sqrt{3}}{126} ,$$

and $\bar{a}_v$ is its conjugate. The complete solution of the zero and first order is then

$$\psi' = X_0 \sin y'' + \lambda_0 (X_1 \sin 2y'' - 2\alpha X_v \sin y'' \sin 2y'') , \qquad (22v)$$

where

$$\begin{aligned}X_v = \left[-\frac{5}{6} + \frac{1}{21}\cos\sqrt{3}x'\right]e^{-x'} + \Bigg[\left(\frac{x'}{3} + \frac{16}{21}\right)\cos\frac{\sqrt{3}x'}{2} \\ + \left(\frac{\sqrt{3}x'}{9} - \frac{25\sqrt{3}}{63}\right)\sin\frac{\sqrt{3}x'}{2}\Bigg]e^{-\frac{x'}{2}} + \Bigg[\frac{1}{42}\cos\frac{\sqrt{3}x'}{2} \\ - \frac{\sqrt{3}}{14}\sin\frac{\sqrt{3}x'}{2}\Bigg]e^{-\frac{3}{2}x'}\end{aligned} \qquad (23v)$$

has been plotted in Fig. 5. The function is very similar to X_1, and the two first order solutions cancel to a large degree. Fig. 6 shows the streamlines according to (22v) for $\alpha = 0.75$, $\lambda_0 = 0.6$. Except for a slight tendency for the north-flowing current to "overshoot," there is little deviation from the zero order solution.

It must be emphasized that the results depend somewhat on our choice of the numerical constants and on the rather arbitrary form of equation (31). This description of the variation in thermocline depth was chosen for its suitability in the computation of higher order terms. Actually our model for the density structure, when combined with the geostrophic equations for the currents, completely specifies the law for the variation in thermocline depth, but the resulting expression is not suitable for the computation of higher order terms (see Fig. 7).

Let us define a stream function Φ, related to the surface mass trans-

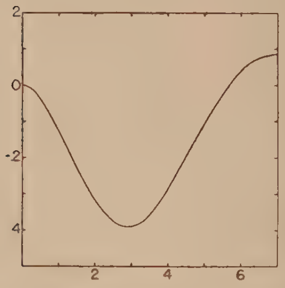

Figure 5. The function X_v (Equation 23v) associated with a variable depth in thermocline.

port $\rho_0 \mathbf{v}_0$ in the same manner as ψ is related to the integrated transport. Then the geostrophic equations, with the aid of (2) and (3), can be written

$$f \nabla \phi = \nabla p_0 = \rho_0 g \nabla h ,$$

$$f \nabla \psi = \int_{-\infty}^{h} \nabla p dz = \frac{5 \rho_0^2 g}{8 \Delta \rho} \nabla h^2 .$$

Solving for h, and neglecting the variation with latitude of the Coriolis' parameter f, leads to

$$h = \frac{f}{\rho_0 g} \phi + h_0 = \sqrt{\frac{8 f \Delta \rho}{5 \rho_0^2 g} \psi + h_0^2} ,$$

where h_0 is the value of h for $\theta = \psi = 0$. It follows from (1) that $H_0 = h_0 \rho_0 / 2 \Delta \rho$ is the depth of the thermocline at the boundary. The above equations can be solved to yield

$$\phi = \frac{\sqrt{1 + a\psi} - 1}{\frac{5}{4} a H_0} , \qquad H = H_0 \sqrt{1 + a\psi} , \qquad \text{(32a, b)}$$

where

$$a = \frac{2f}{5 g \Delta \rho H_0^2} .$$

In order for (31) to be a suitable approximation to (32b), it would be necessary that $\alpha\psi' << 1$ and $a\psi << 1$. Actually $a\psi$ varies from zero to fourteen.

For a numerical example we choose conditions at $y'' = \pi/2$, the approximate latitude of Cape Hatteras. Setting $f = 10^{-4}$ sec^{-1}, $g =$

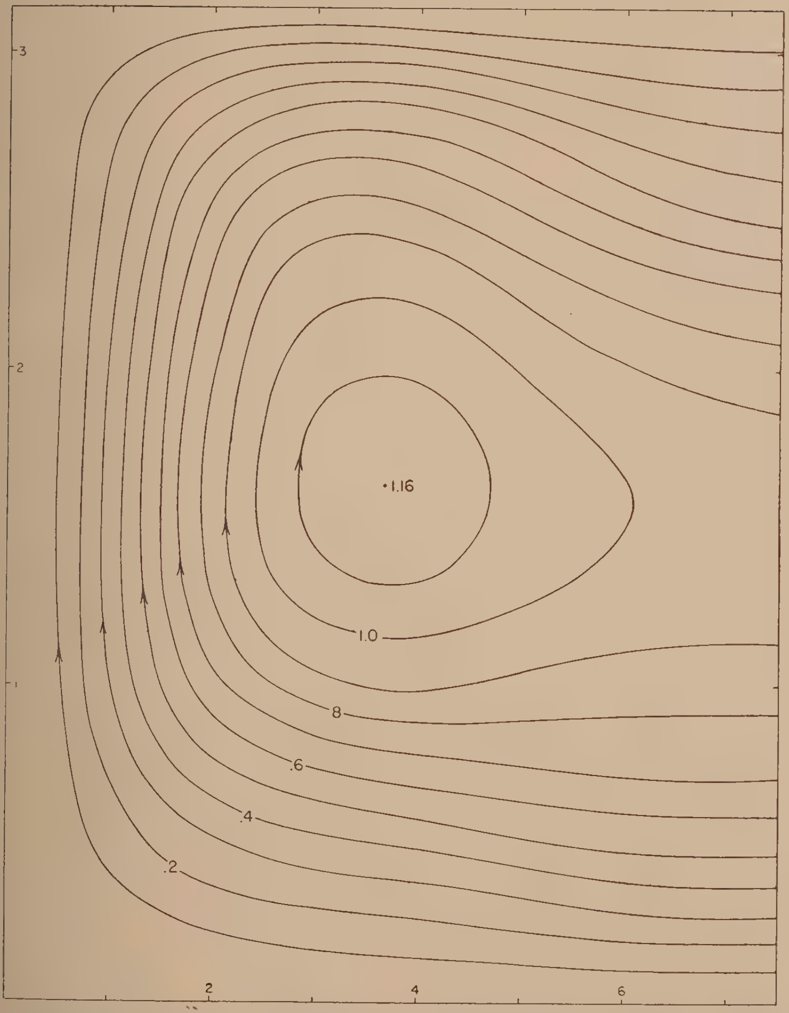

Figure 6. Streamlines of mass transport, ψ', for the combined zero and first order solutions pertaining to a variable depth in thermocline (Equation 22v), assuming $\alpha = 0.75$. The corresponding profile of the thermocline is presented by the dashed curve in the lower portion of Fig. 7.

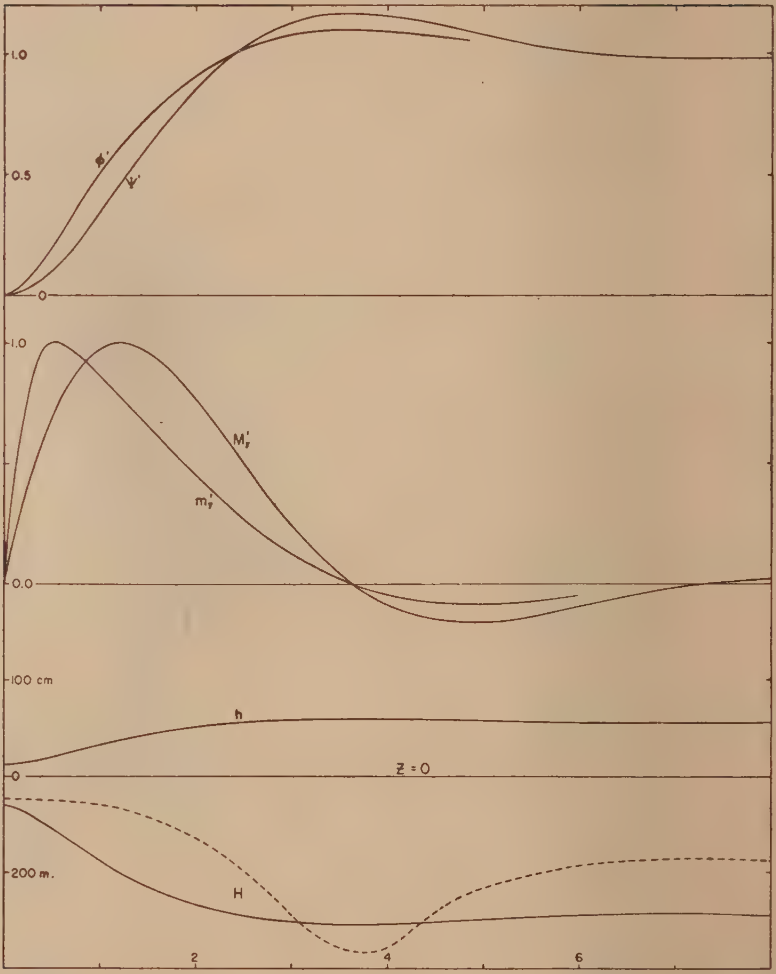

Figure 7. Variation of parameters across the Gulf Stream according to the zero order solution. A unit distance x' equals approximately 50 km. The upper curves denote the surface stream function ϕ' and integrated stream function ψ'. For $\phi' = 1$, $\phi = 4.51 \times 10^8$ g sec^{-1} cm^{-1}; $\psi' = 1$, $\psi = 1.95 \times 10^{13}$ g sec^{-1}. The central curves show the corresponding surface transports and integrated transports. For $m_y' = 1$, $m_y = 55.3$ g sec^{-1} cm^{-2}; $M_y' = 1$; $M_y = 2.13 \times 10^6$ g sec^{-1} cm^{-1}. The lower solid curves represent the surface and thermocline profile according to Equation (32v). The dashed curve is the assumed thermocline according to (31).

$10^3\ g\ \text{sec}^{-2}$, $\Delta\rho = 10^{-3}\ \text{g cm}^{-3}$, $H_0 = 6000$ cm, gives $a = 1.11 \times 10^{-12}\ \text{g}^{-1}$ sec. Furthermore nr = 6, $\Gamma = 0.65$ dynes cm^{-2}, $\beta = 2 \times 10^{-13}\ \text{cm}^{-1}\ \text{sec}^{-1}$. The lower portion of Fig. 7 shows the surface profile and thermocline profile according to equations (1) and (32b). For comparison we have added the thermocline according to (31), assuming that the depth at the boundary is 4,640 cm, which gives the value of 0.6 from equation (30).

The upper curves show the zero solution for ψ' (equation 15) and the corresponding surface stream function according to (32a). The central curves represent the slopes of the upper curves and are proportional to surface current and integrated current, respectively. The distance between maximum current and the left edge is about 25 km at the surface and 60 km for the integrated current. The reason for the displacement of the maximum in the surface current has to do with the variation of the vertical structure across the stream. At the left side (looking downstream) the current is superficial and the surface velocities large. Towards the right the current extends to greater depth, and the surface velocities are relatively small.

CONCLUSIONS

The westward intensification according to the planetary vorticity theory is therefore even more pronounced if surface currents are considered rather than the integrated transport. The width of 25 km for the "cold wall," which corresponds to a value of $A = 2.5 \times 10^7\ \text{cm}^2\ \text{sec}^{-1}$, $p = 0.445$ (Munk and Carrier, 1950: fig. 4), is in agreement with observations in the Hatteras area.

Our examination is unrealistic for a number of reasons. We have assumed the western boundary to be a vertical wall. The bottom rises gradually, of course, and many of the modifications inshore of the Gulf Stream take place over the Continental Shelf. We have also neglected the effect of the indentations in the coastline. Furthermore, the eddy viscosity is taken as constant, whereas in Rossby's theory this coefficient varies along the Stream. Our zero order solution, as represented by the central curves in Fig. 7, resembles the wake stream profile (Rossby, 1936: fig. 4). However, this resemblance is not noticeably improved by the inclusion of higher order terms.

At the outset of this investigation it was hoped that the higher order terms might contain a clue as to the continued concentration of the Gulf Stream long after it has left the American east coast. Another observed feature not contained in the linear solution is the countercurrent inshore (Bumpus and Wehe, 1949). Even though the validity of the higher order terms is in doubt, largely because of their surprisingly strong dependence on the assumed vertical distribution of density, it does not seem likely that these observed features are contained in the higher order terms. There is some essential feature in the dynamics (or thermodynamics) of the Gulf Stream which has not yet been recognized.

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SLICKS, SURFACE FILMS AND INTERNAL WAVES[1]

By

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ABSTRACT

Slicks, or calm streaks on a rippled sea, are often seen on coastal waters and lakes
en the wind is light. They are formed by the ripple-damping action of a surface
n of organic matter which occurs naturally on biologically productive waters.
e ability of films to damp ripples varies radically with the degree of compaction
the film molecules. Such compaction may be caused by horizontally convergent
v in the water surface or by horizontal convergence of the wind stress. The
racteristics of the resultant slicks vary with the agency producing compaction.
e such agency, typical of summer conditions on the California Coast, is a train of
g internal waves in a shallow thermocline. The periodic convergence and diver-
ce of the horizontal component of orbital velocity associated with such waves
duce alternate bands of compaction and extension in the surface film sufficient
cause visible differences in the rippling of the water by a slight breeze. The slicks
arrayed in parallel deployment over successive troughs of the internal wave and
spaced some hundreds of meters apart. Where the wave is progressive, the slicks
progress at the speed of the wave which is of the order of 25 cm/sec. The slicks
propagated as a wave of state traveling in the surface film which itself does not
re the phase motion of the wave but only its local oscillations. This explanation
upported by theory, by model studies and by observations in the field. Internal
ve slicks are not to be confused with the more closely spaced wind-cell slicks which
dominate when the wind force is Beaufort 3 or greater.

Contribution from the Scripps Institution of Oceanography, New Series No. 497

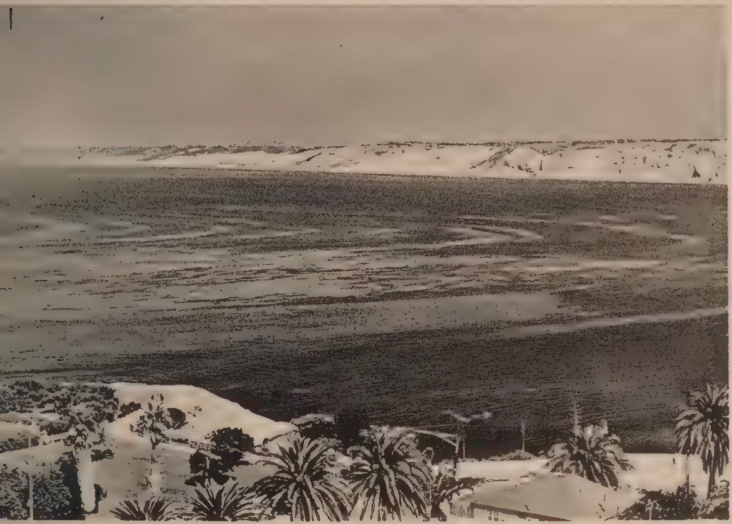
print from *SEARS FOUND. JOURN. MAR. RES.*

INTRODUCTION

Description. Slicks, or calm streaks on rippled water, like th
shown in Fig. 1, are commonly seen on harbor, coastal and lake wat
when the wind is a slight breeze. They have been reported n
California, Samoa, Australia, the Marquesas Islands, the Antarc
icepack, and occasionally in the open sea (Dietz and LaFond, 195
in the Gulf of Panama (Forbes, 1945; Woodcock and Wyman, 194
off the south coast of Borneo (J. D. F. Hardenberg, private communi
tion), and in various Russian seas (Shuleikin, 1935, 1941). W.
Royce of the U. S. Fish and Wildlife Service has photographed th
over the Gulf of Maine, and B. N. Jamison on Lake Tahoe, Californ
At customary angles of observation, slicks appear whiter and brigh
than adjacent zones of blue rippled water. From the air, looki
nearly straight down into the sun's glitter on the sea, they appear
dark streaks. Viewed close at hand, they are sometimes hard to
but can be distinguished by the smooth oily appearance of wavel
and the absence of capillary crispations (Lamb, 1932; Art. 350).
the San Diego region they are observed at all seasons of the year,
in the summer months they are often strikingly distributed in para
array, like bands of alto-cumulus "billow" clouds in the sky; the ca
streaks, 10 to 50 m broad and arranged in congruent sinuous ban
are sometimes many kilometers long and are separated from
another by rippled zones about 300 m wide. In shallow water, su
bands lie roughly parallel to contours of the bottom, but in dee
water they usually lie across the wind direction at various angl
They are visible only when the wind is sufficiently strong to ripple
water. On the other hand, at wind speeds greater than about
m/sec (Beaufort 3, the force required to sway small twigs and
straighten out flags), the slicks break up into a different pattern (Fig.
with narrower bands spaced much closer together and much short
their long axes always oriented nearly along the wind axis in a man
described by Langmuir (1938) and by Woodcock and Wyman (194
who attribute the effect to wind cells. This paper is concerned o
with slicks observed at wind speeds less than 3.4 m/sec, as shown
Fig. 1.

Analysis of the geometry of light reflection from the ocean, by t
author and by Shuleikin (1935, 1941), has shown that the optic
properties of calm streaks are due to the reduction of the avera
angle of reflection (attributed to flattening of the wavelets) and to
complete absence of capillary crispations as observed by Langmu
(1938).

1



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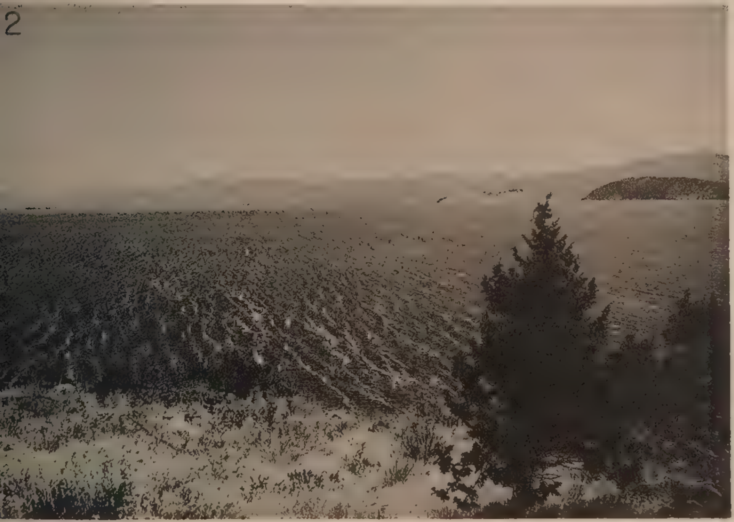

ure 1. A series of internal wave slicks off La Jolla Cove, October 1950.
ure 2. Wind-cell slicks, typical of wind speeds greater than 3.4 m/sec. Photo of Klamath
e, Oregon, in July 1949 by R. Revelle.

Wave-like Nature of the Phenomenon. Observations of an hou
more, sometimes with the aid of single exposure cinematograph
spaced intervals, have frequently revealed a most remarkable prop
of the streaks, namely, that they move at right angles to their
axes at a regular rate of from 10 to 40 cm/sec, in the manner of l
period swell but very much more slowly (Ewing, 1950). This velo
is characteristic of internal waves known to exist in the shal
thermocline of summer. The wave-like nature of this motio
revealed by the fact that dye or paper placed ahead of an advan
slick does not move along with it but is overtaken, passed and
behind nearly in its original location, thus showing that a chang
the state of the sea surface which is sufficient to calm ripples is b
propagated without dependence on steady flow of the water itself.

The Surface Film. The physical medium in which a change of s
occurs will be shown to be a contaminating surface film of org
composition, such as is known to inhibit the formation of rip
(Aitken, 1884; Gibson, G. E., 1944) and to damp those already for
(Pockels, 1891). Such a film, since it reduces the surface tensio
water, spreads until it is one molecule thick (about 6 x 10^{-7} cm).
spread still further by some extraneous agency, the film breaks
probably into discontinuous patches or islands of coherent mate
some millimeters in diameter; at the same time it loses its damp
effect on ripples and its ability to depress the surface tension (Fig.
point D). If the area occupied by the over-expanded film is redu
by steady contraction, the film first begins to resist the contraction
an elastic manner (Fig. 3, point C); next it regains its ripple-dampi
ability and begins to reduce the surface tension; and then, as
islands fuse to form a continuous film (Fig. 3, point A) it abrup
becomes nearly as imcompressible as the same material in b
(Devaux, 1914), since its molecules are then standing close-pack
like sticks of chalk in a box (Langmuir, 1917).[2]

The Effect of Surface and Internal Waves. The discrete islands of
over-expanded film freely share the motion of water particles in
surface, and in consequence they may be crowded together to form
continuous ripple-damping film by horizontal convergence. T
film may be broken up in turn if expanded by divergence. Su
rhythmic convergence and divergence occur whenever a water surfa
is being alternately raised and lowered by a train of surface wav
and it has been shown by Hardman (1941) that, on lake water som
what contaminated by naturally occurring organic matter, the surfa
tension alternately falls and rises during the passage of crests a

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[2] For a general review of the properties of surface films, see Adam, 1941.

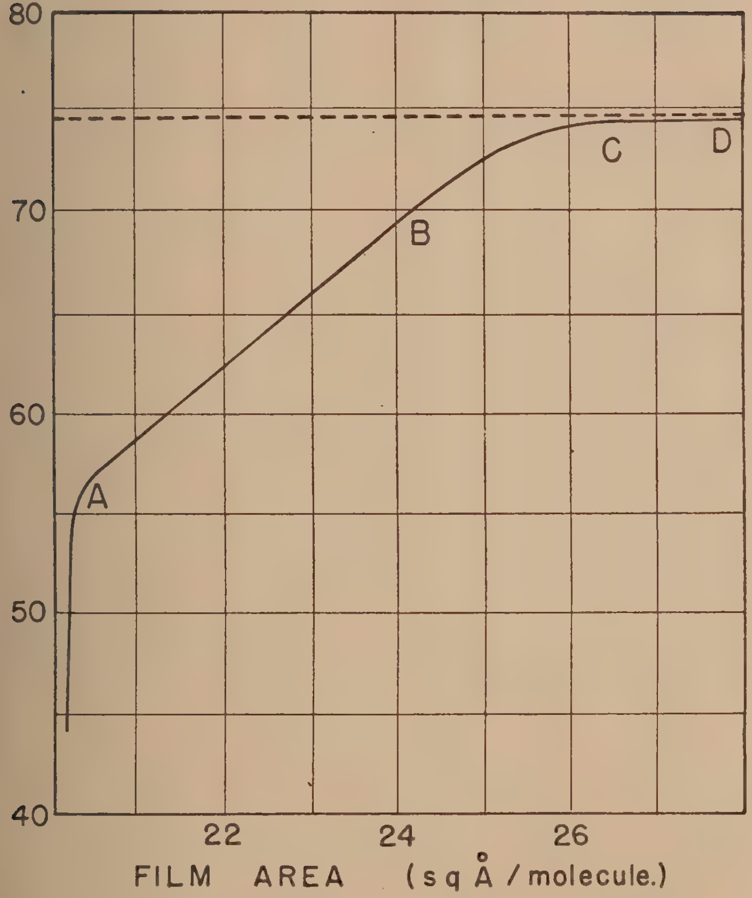

Figure 3. Variation of surface tension with degree of extension for typical film of fatty id on water. The dashed line shows the surface tension of pure water. Redrawn from lam, 1941.

oughs of surface gravity waves. This variation in surface tension ust be accompanied by changes in the rippling, but the rapid changes slope of the surface and the brevity of the cycle are unfavorable for e detection of such changes by visual means. On the other hand it known that, over a long internal wave in a shallow thermocline, horiontal convergence and divergence occur throughout the upper layer ver the descending and rising phases of the wave respectively (Lamb, 1932; Sverdrup, et al., 1946). Analysis of the orbital particle motion associated with a long internal wave, to be presented herewith, shows that, if the amplitude of the wave be a sufficiently large fraction of the thermocline depth, say about ¼, the alternate extension and compaction of the surface is quite sufficient to develop the full variation in the degree of ripple-damping of which a given surface film is capable. At the same time, the slope of the surface, and hence the direction from which it reflects light, is disturbed to an altogether negligible degree by the internal wave, and the durations of the expanded and compacted states of the film are much longer than in the case of a surface wave of similar dimensions. The bands of damped and undamped ripples over the trough and crest respectively of the internal wave should therefore be easily seen and distinguished. These deductions have been unequivocally supported by model studies undertaken by the writer, described herewith. Likewise, field studies have shown long internal waves of suitable dimensions to be present in the San Diego region during the summer months (Ufford, 1947a), and a bathythermographic section taken across a series of parallel slicks shows that the calm streaks lie over troughs, the rippled zones over crests, of a train of such internal waves (Ewing, 1950). Finally, the hypothesis that natural calm streaks are caused by a film in a state of compaction is supported by measurement of the lowering of surface tension in slicks (ZoBell, 1946) by means of a rapid field method dependent on the spreading power of various solutions (Adam, 1937) and by measurements of the absolute surface tension with a du Nouy type tensimeter (Shuleikin, 1935, 1941; Dietz and LaFond, 1950).

EXPERIMENTS

Chemical Analysis of Natural Marine Film. Because of its fragility, the contaminating film occurring naturally on the ocean is ordinarily collected with difficulty. However, a slick is occasionally found in which the compaction has exceeded the critical limit. This results in the crumpling and foaming of the film in the manner described by Devaux (1914) so that a narrow band of heavy scum which has lost its elasticity is formed. Samples of such scum were collected from the Scripps Institution Pier, which projects into the open sea far from any harbor. The scum was skimmed off the water into a bucket and transferred to a separatory funnel. Even the gentlest handling destabilizes some of the suspended matter, this then permitting the escape of air bubbles and throwing down the heavier solids. The solid matter was filtered out, drawn off, dried, and weighed. E. F. Corcoran of the Biochemistry Division, Scripps Institution of Oceanography, assayed the filtered and dried solids for total carbon, using ret combustion with chromic acid (Waksman, 1936). The solid naterial was found to contain about 27% organic matter. No attempt vas made to analyze the liquid and gaseous phases.

Contamination of the sea surface by surface-active substances of a lass known commonly to have the properties on which ripple-damping epends (Adam, 1941: 50–51) strongly supports the hypothesis that alm streaks are usually due to the presence of a surface-active film nd are only indirectly related to other agencies, such as variations in he flow of wind or water. This conclusion is in accord with that of huleikin (1935, 1941).

In view of the generally low concentration of organic matter in the ea, the high organic content of the film substance should be of interest o biologists, particularly because of reports that slicks on the ocean re sometimes zones of heavy concentration of zooplankton (Thomp-on, 1862; Beebe, 1926a). On the other hand, the neuston bacteria f the ocean (i. e. those depending on the surface film for support) are ometimes highly concentrated in slicks but more often show no articular relation to them (ZoBell, 1946). This variability may be ue to variation in the type of slick. Those slicks associated with airly permanent features of the water movement (for example, those ormed where rivers flow into the sea) are generally distinguishable by heir content of floating detritus. They probably promote production f bacteria due to the enrichment of the surface by accumulation of rganic matter. On the other hand, in slicks of the type considered ere, i. e. those that are the result of a traveling wave of film-compres-ion, no such increase of productivity would be expected because the ffect on the surface film is transitory. In fact, the periodic fall of urface tension might be a hazard to organisms depending on the urface for support.

Horizontal Convergence Over Internal Waves. The simplest type of nternal wave (Fig. 4) is that of Stokes (Lamb, 1932; Sverdrup, et al., 946), where it is assumed that a fluid layer of uniform density ρ' lies ver a heavier layer of uniform density ρ, their respective thicknesses eing h' and h. Ufford (1947b) has shown that this simple wave is a atisfactory approximation to summer conditions in the San Diego egion. As with surface waves, the primary features of internal waves epend strongly on the relation of wave length to water depth, in this ase to the dimensions h' and h. We shall concern ourselves only with vaves long in relation to h', since internal waves of other dimensions ave little effect at the upper surface. Compared to surface waves, he potential energy associated with a given deformation of the inter-ace is much reduced due to the presence of the overlying layer, while conversely the inertia of the system as a whole is increased. Consequently, compared to a surface wave of equal length, the velocity of propagation of an internal wave is reduced by a factor (depending on the relative densities of the two layers) which in the ocean is usually of the order of $10^{-3/2}$, i. e. about 1/30.

The streamlines and trajectories of the motion of individual wate particles are shown in Fig. 4, both for a standing wave such as can b produced conveniently in a laboratory model and for a progressive wave such as is usually found in nature. The orbital particle motio

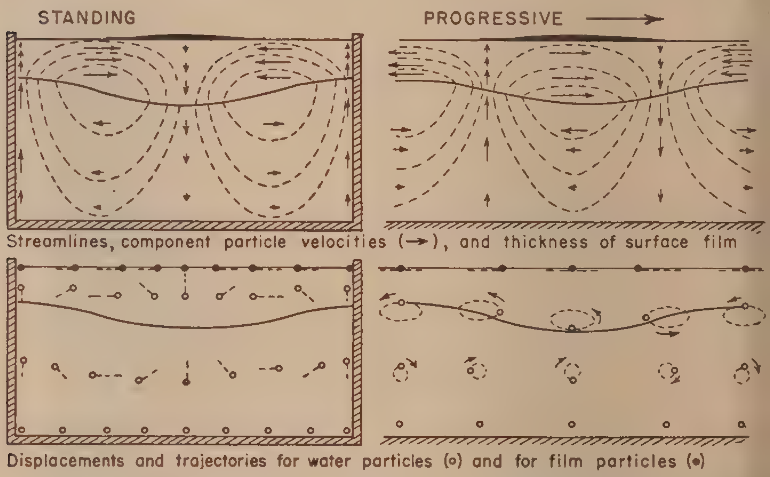
STANDING
PROGRESSIVE
Streamlines, component particle velocities (→), and thickness of surface film
Displacements and trajectories for water particles (∘) and for film particles (•)

Figure 4. Long internal waves. (The extreme values of the flow and of the deformatio of the interface shown together in the upper left diagram do not occur simultaneously.)

is in opposite sense in the two layers. In the upper layer the horizontal component of particle velocity, which is nearly uniform from the interface to the surface, is divergent over the rising phase of the wave and convergent over the descending phase. It can be seen by examining the distribution of surface particles in their orbits that in both types of wave the particles are most closely crowded over the trough and most dispersed over the crest of the wave. Were this superficial layer a mono-molecular film of hydrophilic substance, the condition over the trough would be one of compaction, in which ripples would be most speedily damped. If, on the other hand, the superficial film were of appreciable thickness, as in the case of a heavy coating of oil, it would be considerably thickened in this same region. As shown in Fig. 4, there is a slight vertical disturbance at the surface which is exactly out of phase with the displacement at the interface, this displacement being required to satisfy the condition of uniform pressure along the bottom. However, the amplitude of the surface wave, which has been exaggerated in Fig. 4, is negligible in the model and in nature.

In so far as the effect on a surface film is concerned, the chief difference between standing and progressive waves is that in a standing wave the horizontal motion vanishes over the crest and trough whereas in the progressive wave it is at a maximum at these positions. Over a standing wave in a tank, a band of compaction forms alternately at the center and at the two ends of the tank. At the center, the band alternately forms by accretion from both directions during the descending phase of the wave, and then it is dispersed by scattering along each edge of the band during the rising phase. On the other hand, in the progressive wave, the zone of compaction is propagated with the same velocity as the internal wave, the zone being continuously advanced by accretion along its leading edge and scattering along its trailing edge. Over the trough, the particles are moving in the direction of wave propagation with a horizontal component of velocity

$$u' = \frac{a}{h'} c, \tag{1}$$

where c is the velocity of wave propagation, a the amplitude at the interface. A particle halfway between the crest and oncoming trough is at rest and is approached by the particles in motion over the trough. It is also accelerated so that by the time it is overtaken by the center of the zone of compaction it will have its maximum horizontal velocity, u', which is, however, less than c. As it is passed by the wave, it loses velocity and drops out the rear of the zone of compaction, coming to rest at a point somewhat ahead of its initial one. During the remaining half-cycle over the next wave crest it will be returned to its original position by reversal of the previous motion.

Neglecting second order terms (Lamb, 1932: Art. 228), the maximum horizontal displacement of the particles over either progressive or standing waves is given by a/kh', where k is the wave number in radians per unit of length. The amount by which the displacements from the mean positions of two neighboring particles differ is equivalent to the degree of relative extension of the surface between them, which, to the same approximation, has a/h' for its maximum value. Since the state of the surface film, and consequently its ability to damp ripples, depends on its relative compaction, a model will be similar to its prototype in this respect if the geometric similarity a/h' is preserved.

TABLE 1. Kinematics of Long Internal Waves and Effect on Ripple Damping

PARAMETER	Symbol	Unit	STANDING WAVE			PROGRESSIVE WAVE		
			FORMULA	Maximum Values in Model		FORMULA	Maximum Values Typical Ocean Wave	
				Calculated	Measured		Calculated	Measured
Potential Upper Layer Lower Layer	 ϕ' ϕ		$(A \cosh ky + B \sinh ky) \cos kx e^{i\sigma t}$ $C \cosh k(y - h) \cos kx e^{i\sigma t}$			$(A \cosh ky + B \sinh ky)\, e^{i(kx-\sigma t)}$ $C \cosh k(y - h)\, e^{i(kx-\sigma t)}$		
Density Upper Layer Lower Layer	 ρ' ρ	 g/cm³ g/cm³			 0.998 1.029			 1.0255 1.0244
Thickness Upper Layer Lower Layer	 h' h	 cm cm			 8 24			 735 1000
Wavelength	Λ	cm			75			36,500
Wave Number	k		$2\pi/\Lambda$	.084		$2\pi/\Lambda$	.00017	
Period		sec	$2\pi/\sigma$	6.8	7.1	Λ/c	1750	1900
Frequency	σ	rad/s	(see Lamb 1932: art 231)	.941	.885	ck	.0036	.0033
Propagation Velocity	c	cm/s	σ/k	11.2	10.5	$\{g \cdot hh'/(h+h') \cdot (\rho - \rho')/\rho\}^{1/2}$	21	19
Displacement of Interface	η	cm	$a \cos kx \cos \sigma t$		2	$a \cos (kx - \sigma t)$		200
Horizontal Component of Particle Velocity	u'	cm/s	$-(a/h')c \sin kx \sin \sigma t$	2.7	4.0	$-(a/h')\, c \cos (kx - \sigma t)$	5.8	
Horizontal Displacement of Surface Particle	ξ	cm	$(a/kh') \sin kx \cos \sigma t$	3.0	3.1	$(a/kh') \sin (kx - \sigma t)$	1600	
Compaction of Surface Film			$-(a/h') \cos kx \cos \sigma t$	.25	(see Fig. 8)	$-(a/h') \cos (kx - \sigma t)$	.28	
Ripple Wavelength	λ	cm			.83	$2\pi\, (T/\rho g \cdot \Lambda/\lambda)^{1/2}$	.3	
Modulus of Decay Film Compact Film Extended	 τ' τ	 sec sec	 $.322\, \lambda^{1.75}$ (see Fig. 5) $.712\, \lambda^2$ (see Fig. 5)	 .23 .49	.23	 $.322\, \lambda^{1.75}$ (see Fig. 5) $.712\, \lambda^2$ (see Fig. 5)	 .040 .064	

The various parameters discussed above are summarized in Table I or both a standing and a progressive wave. The numerical results ave to do with specific examples of a standing wave in a model and a rogressive wave in the ocean which will be described presently. The nalysis of Table I follows Lamb (1932: Art. 231) and Sverdrup t al. (1946: 585–589).

Ripple Damping. The precise relation between film compaction nd ripple damping cannot be calculated, because there is available either a complete theory relating damping to the state of the film nor irect empiric knowledge of changes of state with extension for a aturally occurring film.

For waves whose energy is dissipated by viscosity in the absence of nterference from an elastic surface film, Stokes calculated a modulus f decay $\tau = \frac{1}{2}\upsilon k^2$, where υ is the kinematic viscosity and τ is defined y the relation

$$a = a_0 e^{-t/\tau}, \tag{2}$$

vhere a_0 is the initial amplitude and a is the amplitude at any later ime t. For water, and in terms of wavelength, the numerical value f τ is given by

$$\tau = 0.712\lambda^2 \text{ seconds} \tag{3}$$

f λ, the wavelength, is expressed in centimeters (Lamb, 1932: Art 348).

Where the surface, instead of being quite free, is elastic because of ontamination by a film in a critical state of extension, wave energy nust be dissipated at an increased rate by the alternating tangential lrag on the water as its surface is contracted and expanded by the rests and troughs of the waves (Reynolds, 1880). Lamb (1932: Art 51) attempted to "submit this explanation, to a certain extent, to the est of calculation." For wavelengths between a fraction of a millineter and several meters, the modulus of decay, τ', is $(8/\upsilon k^2\sigma)^{1/2}$, vhere σ is the frequency in radians per second. The numerical value of τ' in seconds may be computed from the wavelength in centimeters y the following formulae:

$$\text{for capillary ripples } \tau' = 0.322\,\lambda^{1.75} \text{ seconds;} \tag{4a}$$

$$\text{for gravity waves } \tau' = 0.375\,\Lambda^{1.25} \text{ seconds.} \tag{4b}$$

For longer wavelengths viscous damping is negligible and for extremely ninute ripples the calculation fails because the assumptions on which t is based are violated. Curves of τ and of τ', together with their atio τ'/τ, are given in Fig. 5.

Reynolds' explanation (Lamb, 1895: Art 304) is based on the sup-

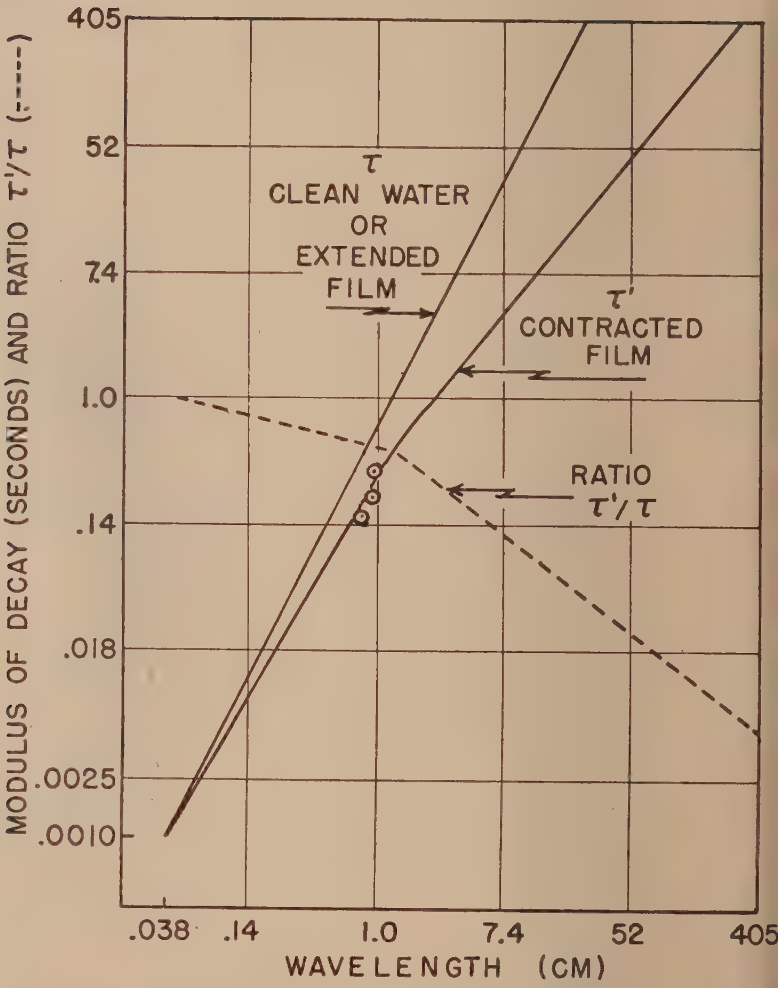

Figure 5. The modulus of decay for various wavelengths for clean water, or under an extended film (τ) and under a contracted film (τ'). The dashed line shows their ratio τ'/τ. The circled points are values observed in model experiments.

position that the surface tension varies by an amount proportional to the extension, so that

$$T = T_0\left(1 + f\frac{d\xi}{dx}\right), \qquad (5)$$

vhere T_0 is the tension in the undisturbed state, ξ is the horizontal lisplacement of a surface particle, and f is a numerical coefficient roportional to the slope of the surface tension curve (Fig. 3). But, o quote Lamb, the elasticity of the film has the effect "of practically nnulling the horizontal motion at the surface. The dissipation is herefore (within limits) independent of the precise value of f." Since he film is elastic only when the surface tension varies with the degree f compaction, it follows that τ applies to film states where f vanishes, hat is, to the right of point C in Fig. 3. Likewise, τ' must apply where is finite, as in the region to the left of point C, and must be constant vhere f is constant, that is to the left of B. It can be seen that the full ange of damping rates between τ and τ' must be exhibited within a elatively narrow range of film extension corresponding to the shoulder f the curve between points B and C. This region is that in which the ilm loses its depressing effect on surface tension and hence its spreading endency. Films in nature, if they are in equilibrium with the surface ension of water, must therefore tend to be nearly in a critical state of xtension with regard to ripple damping.

The only previous experimental test of these equations appears to be hat of Pockels (1891), who found a constant high damping rate, quivalent to τ', for films compacted beyond the point B in Fig. 3 vhere surface tension falls rapidly and a constant low damping rate, quivalent to τ, for films compacted to any degree less than half this mount. The damping times varied by a factor of 5.7 between these xtreme conditions.

For any particular film substance, the shape of the shoulder of the urve of surface tension versus extension varies with the chemical omposition and temperature of the substance and with the pH and ther ion-concentrations of the underlying fluid. For the film found n the ocean, the applicable curve could be determined only by delicate aboratory methods that are not readily applied in the field (Adam, 941: 27–35). However, the Pockels results, which are for an unspecified film-substance, are typical of a wide variety of organic ompounds (Adam, 1941: 50–51). Therefore, it seems reasonable to ssume that, for a film initially in equilibrium with the surface tension f water, an extension and contraction of the order of ± 25% will produce the full range of damping effect of which the film is capable, the ratio of maximum and minimum rates being, from (3) and (4a),

$$\frac{\tau'}{\tau} = 0.45\lambda^{-1/4}. \tag{6}$$

Finally, in order to examine the ability of wind of a given speed to maintain ripples in spite of viscous damping, W. H. Munk of the

Scripps Institution has made calculations (following a method due i part to Jeffreys; see Lamb, 1932: Art 348) that show the effect fo various wind speeds of a contaminating film in its extended (τ) an contracted (τ') state. His main results, kindly made available as Fig 6, are that the minimum wind speed for growth of waves is 245 cm/se when the surface is elastic (film compacted) compared to 110 cm/se when the surface is free (film absent or extended). In each case the first waves to achieve stability at minimum wind velocities are gravit waves. Increased wind speeds produce a spectrum of stable waves

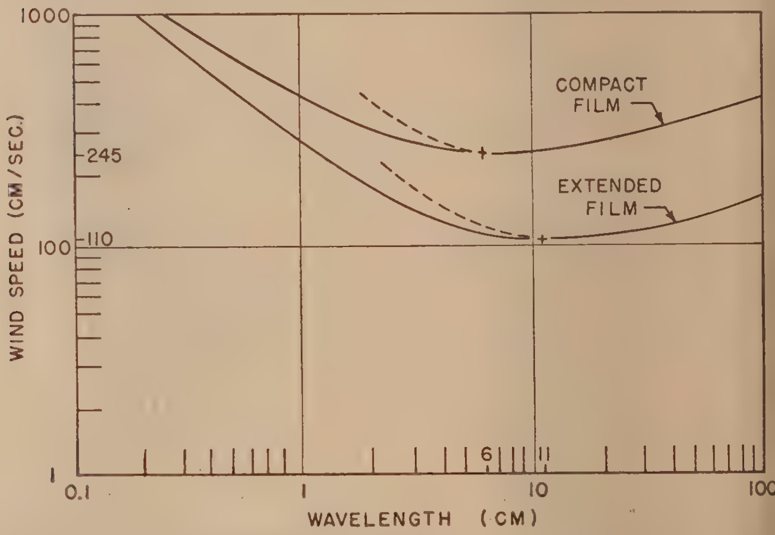

Figure 6. Limits of the spectrum of stable waves (————) and the "preferred" wav length (– – – –) for various wind speeds.

Corresponding to each wind speed, waves of a particular "preferred length will grow fastest. The preferred wavelength is shorter a higher wind speeds.

Summary and Hypothesis. The foregoing analysis leads to the hypothesis that whenever a long internal wave exists at the interface between two layers of water with an amplitude exceeding ¼ of the thickness of the upper layer, such a wave will produce over its troughs horizontal convergence at the upper surface sufficient to bring a organic surface film into a state of compaction where ripples will be damped at the maximum rate which the film can cause; conversely, i will produce over its crests divergence sufficient to extend the film to a

ate where the rate of ripple-damping is minimal. The differences in
ppling will be plainly evident, whether the ripples are produced at
ne point by a mechanical vibrator (as in a model experiment) or
niformly over a given area by wind blowing at a speed of 110 to 340
m/sec. If the internal wave is a standing wave, as in a model, calm
ones will appear and vanish alternately over each antinodal point of
e wave, the phase being opposite at adjacent antinodes, with the
alm phase coinciding at each point with the depression of the inter-
ace. If the internal wave is progressive, as in nature, calm zones will
emain continuously over the troughs of the wave and will themselves
ove as a wave of state along the surface film, their speed being
overned by the propagation velocity of the internal wave.

The foregoing hypothesis has been put to the test of experiment
nd observation.

Model Experiments. In order to study the effect of an internal wave
n a surface film, a model was set up in the laboratory. It consisted of
standard aquarium containing a layer of clear tap water over an 8%
olution of cane sugar (specific gravity 1.029) which was colored red
ith photographic opaque. A glass plate, slightly narrower than the
ank and somewhat more than one-third its length, was laid hori-
ontally on wire supports 6.5 cm. beneath the surface of the lower
ayer. A synchronous motor, connected to a suitable variable speed-
eduction transmission, was used to rock the glass plate through an
ngle of 10° about its median horizontal axis, which was transverse to
he aquarium and located ¼ the length of the aquarium from one end.
his gentle motion, when the period was critically adjusted, produced a
tanding wave with an amplitude of 2 cm (4 cm height) and a fairly
inusoidal profile. By suitable change of the period, a half-wave or a
hree-halves wave was easily produced. Once established, the strati-
cation is very stable and the layers remain distinct for several days.
he upper layer can be floated onto the lower one by allowing the
ater to drip from a separatory funnel onto a supported watch glass,
r, if care be taken to make a uniform sugar solution in advance, the
ower layer can be run in below the upper layer. Lacking a suitable
otor to govern the wave, the glass plate could be rocked by hand, but
n this case it would be better to use a less dense sugar solution so that
he period would be slower and less critical. When first examined, the
ree surface may be found so strongly contaminated as to be nearly
nextensible, that is, in the state represented in Fig. 3, to the left of
oint B. (The same condition is commonly observed at the surface of
ewly brewed China tea.) The surface is easily cleaned by floating
bsorbent paper upon it and removing it with a stripping motion.
light dusting of talc revealed the horizontal motion of the surface as

well as the cycles of convergence and divergence in a spectacular way, the converging particles of talc coming together with the appearance of shock at the limiting minimum area, point A in Fig. 3. Any oil of vegetable or animal origin will restore the necessary amount of contamination to the surface should it be cleaned to an unwanted degree.

A second effect of the internal wave is the periodic variation of the thickness of the superficial layer. This was studied by placing a rather heavy film of oil on the surface, which then loses its horizontal motion but exhibits interference colors that vary through the primary visible spectrum and sometimes on into the secondary one with each cycle of the internal wave, thus showing a change of thickness of some thousand Ångstrom units.

To test the effect of film compaction on ripple damping, advantage was taken of a mechanical device designed by E. A. Williams of Santa Barbara College. It consisted of a light horizontal lucite bar 15 cm long of inverted triangular section 5 mm at the base, attached by a short vertical tube to the diaphragm of a small magnetic radio speaker. The speaker was driven by an audio-oscillator through a power amplifier at frequencies that could be varied from 10 to 60 cycles/sec. The amplitude could also be controlled. With the lucite bar just touching the water surface and with the speaker driven at 36 cycles, a regular train of 8 mm ripples could easily be seen crossing the aquarium when the surface was nearly clean. They were nearly obliterated by larger amounts of contamination. In order to photograph these minute ripples, a photoflood lamp was directed at the surface so that the shape and uniformity of its reflection could be observed. In the absence of ripples, the reflection was quite round and specular. On the other hand, when ripples were present, they broke up the reflection into corrugations within an envelope which was elongated along the axis of the ripple train. Since the ripples were subject to damping during their passage across the reflection, those to the left were steeper than those to the right, thus resulting in greater elongation to the left and hence in the egg-shaped envelopes shown in Fig. 7. The rate of damping was calculated from the asymmetry of the envelope in the compact phase and it was found to be in fair agreement with the values calculated for τ' by means of equation (4a). The experimental values for three separate cycles of the internal wave are shown as circled points in Fig. 5.

The relations betweeen the internal wave, the extension of the surface, and the rippling are shown in Fig. 7, where the reduction of rippling over the trough of the internal wave is clearly evident. The relation between the calculated and the actual dimensions of the wave motion, film extension and ripple damping are entered in Table I.

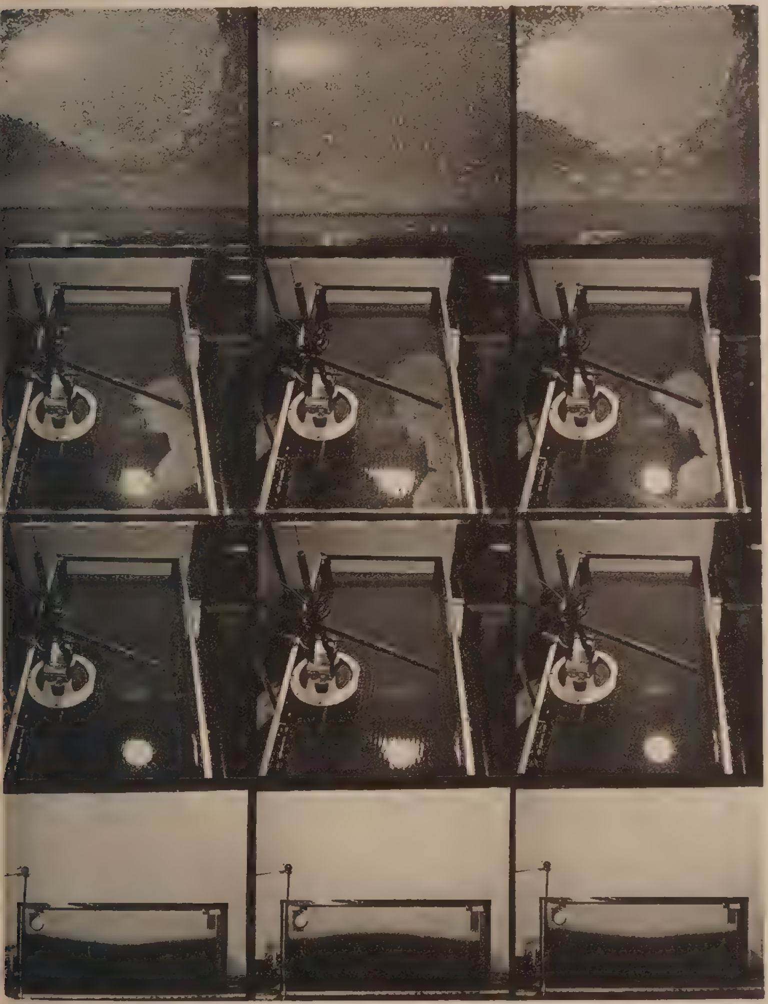

Figure 7. The model in action. Columns are matched and represent a sequence of exposures at intervals of ½ wave period. Top row, particles of talc on the surface in alternate states of compaction and extension; second row, film compaction and ripple damping; third row, high and low rates of damping; bottom row, alternating phases of the internal wave.

A cine film of the surface was used to measure, frame by frame, both the extension of the film, as revealed by the separation of two arbitrarily chosen neighboring particles of talc, and the simultaneous steepness of the ripples, as revealed by the elongation of the envelope of light reflection to the left. The result is presented in Fig. 8, where the abrupt change of slope of the curves which show the separation of the particles indicates that there was a definite limit to the degree of compaction that the film would tolerate. The central curve, which shows the time variation of envelope extension, reveals that the ripples were fully damped at a compaction somewhat less than the maximum.

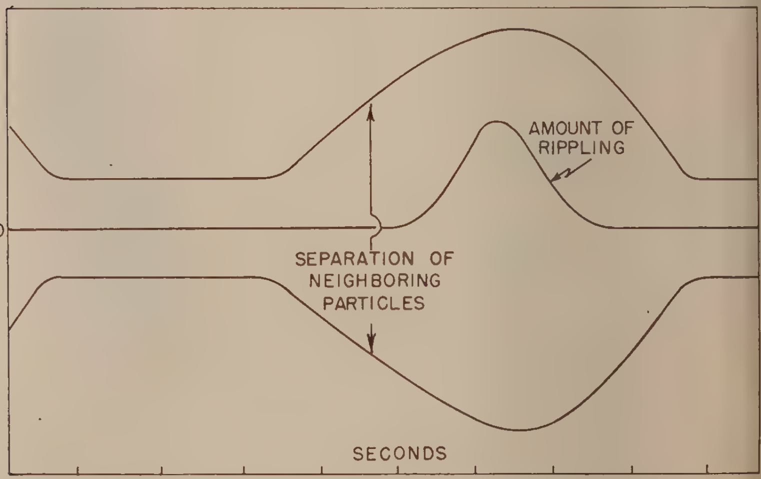

Figure 8. Extension and contraction of a surface film over a standing internal wav showing the effect of limited film compressibility and its relation to ripple damping.

This is in agreement with Pockels' results, and it shows that considerable damping effect would have been produced by an internal wave o a/h' ratio even smaller than ¼.

Finally, although it is probably implicitly clear to the reader tha the transfer of the state of film compaction between adjacent antinode of the wave was wave-like in character, yet it must be explicitl stated that such was the case. For the wave detailed in Table I, th shift of calm phase from the center to the ends of the model was over distance of 37.5 cm, yet the maximum horizontal displacement o individual particles of the surface film was observed to be only 3.1 cm thus proving that the ripple-damping effect was truly a change o state which was propagated independently of any but small oscillaons of the medium. For reasons which will appear presently, events nature are not favorable to such exact observation. However, it is easonable to assume that, under similar kinematic conditions, the ehavior of the sea surface is similar to that of the model surface, with ne difference that, as in the ocean we expect to find progressive rather nan standing internal waves so, correspondingly, we shall expect the ave of film compaction on the ocean to be propagated with a steady elocity instead of vanishing at one antinode while simultaneously ppearing at the adjacent ones.

FIELD OBSERVATIONS

Long Internal Waves in the Sea. Turning now to the ocean or to rge lakes to see whether internal waves have similar effects on the rger natural scale, it is easily established that the condition $a/h' \geqslant 1/4$

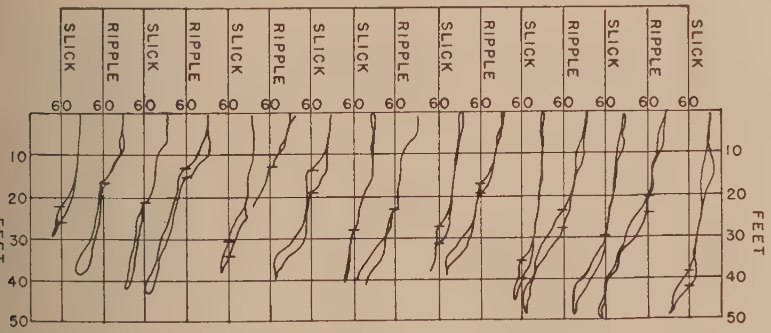

Figure 9. A series of bathythermograms taken in rapid succession from a moving ship ogether with simultaneous observations of slicks, showing the elevations and depressions of 0° F isotherm in relation to the presence of ripples or slicks at the sea surface.

s satisfied in the summer when the thermocline is shallow. On June 7, 1949, near San Diego, the writer used a bathythermograph (Spilaus, 1938) to measure an internal wave with an average amplitude of 00 cm about a mean depth of 735 cm, for which the ratio a/h' is 0.27 Fig. 9). Ufford (1947a), using a different method, measured in the ame region and season (but at an unreported depth) an internal wave f 16 min period with a length of 330 m and an amplitude of 228 cm, nd another of 12 min period, 130 m length and 152 cm amplitude. These were progressive waves which would produce the particle notion shown in Fig. 4. The calculated velocities associated with uch a wave, together with the displacement of particles in the surface and the resulting film compaction, are shown in Table I, where, for easy comparison, these calculations are placed alongside those for the experimental tank. It is seen that compaction, the parameter on which ripple-damping depends, is little altered in going from model to prototype. Therefore, one would expect to find parallel streaks of calm over the successive troughs of a train of such internal waves which would move along the surface at a velocity equal to the propagation velocity of the internal wave. The occurrence of such slicks was reported by the author (Ewing, 1950) and is illustrated in Fig. 1. The superficial resemblance to long-crested swell is apparent.

Bathythermograph Observations. In order to test the relation of such a series of calm streaks to internal waves, a temperature section was made, using a bathythermograph specially modified for observations shallower than 50 feet (15 m). The section was taken from a ship moving along a track normal to the long axes of the streaks and roughly at right angles to the coastline. The instrument was lowered successively in each slick and in the approximate center of each intervening rippled zone, starting with the inshore slick of the series. The resulting traces are arrayed in their proper order in Fig. 9 where, for the sake of simplicity, only the depth of the 60° F (15°.6 C) isotherm is shown. It will be seen that under each calm streak this isotherm was depressed relative to its depth under adjacent rippled zones. The alternate rise and fall of the isotherm is interpreted to correspond to the crests and troughs of a train of internal waves. The average depth of the isotherm is 24 ft (735 cm), and the average vertical displacement, corresponding to the amplitude of the wave, is ± 6.6 ft (200 cm), giving the ratio $a/h' = 0.27$, as noted above. Thus it is shown that, where natural slicks are arranged in a series of equidistant lines over a long internal wave, they are situated over the troughs of the wave, as in the model.

The Distance between Slicks. On the proposed hypothesis, the distance between the calm streaks of a series should correspond to the wavelength of the accompanying internal wave. The interslick interval of a series (which included those previously examined by bathythermograph) was measured by sailing across the slicks in the direction described above, noting the time of passage through each successive slick on the moving tape of a sonic depth recorder. Inside the 85 m contour of water depth, the slicks were fairly evenly spaced at intervals varying from 395 to 630 m with an average interval of 486 m. These may be compared as to magnitude with the wavelengths of the two internal waves measured by Ufford in July 1945, namely 330 m and 130 m.

Along the slope of a sudden declevity beyond the 85 m contour, the icks were crowded together at an average interval of 102 m. A hotograph made by W. F. Royce shows a similar terminal aggregation f streaks in one pronounced band; Forbes (1945) has reported the ame distribution in Panama Bay. These may mark regions in which hort period internal waves are generated. Indeed, a mechanism hereby internal waves may be generated by a tidal current running gainst a submerged shelf has been proposed and experimentally emonstrated by Zeilon (1934).

Propagation and Refraction. In order to see whether serially rranged calm streaks move with the velocity of propagation of proressive internal waves, studies were made with a motion picture amera by exposing film at a rate of six frames per minute. When this lm is projected at 16 frames per second, the calm streaks are seen to rogress sideways to their long axes, as long crested swells do. The ate of progress was found to be 22 cm/sec on May 17, 1949 and 16 m/sec on June 13, 1949. These velocities are comparable to those easured by Ufford (1947a) for two July internal waves which were 5 and 18.5 cm/sec.

Since the propagation of long internal waves is dependent on depth ccording to the equation

$$c^2 = g\,\frac{hh'}{h+h'}\,\frac{\rho-\rho'}{\rho}\,, \qquad (7)$$

here g is the acceleration of gravity, internal waves must be reacted so as to approach parallelism to the contours of both the botom and the thermocline (Munk and Traylor, 1947). Consequently, ff the coast of San Diego, where the bottom and the thermocline ently slope away from shore, internal waves in shallow water should e oriented roughly parallel to the coast. This tendency is reflected the orientation of slicks which parallel the shore regardless of wind irection, provided the wind is light. Where the bottom contours re sharply curved, as over a canyon, the internal waves should be onvex toward shore. Correspondingly, surface streaks over La olla canyon have been observed to have this configuration, each one owed congruently so that it would fit its neighbors if placed in contact.

The Reflection of Light from the Sky. The intuitive supposition that he optical effect of slicks is due to decrease in wave steepness can be igorously examined by observing the sun's glitter path on the water. Iulburt (1934) has shown that the width of the path depends on wave teepness. Observation reveals that where a calm streak crosses the un's path it reduces the path width to zero. Hulburt has also shown that the light reflected by the sea, when ruffled by a 5 to 20 knot wind, is from an average altitude of 30° above the horizon. Consequently, on a clear day a rippled sea is quite blue. In slicks, however where the wave steepness is less, the light is reflected from near the horizon, so that in contrast to the blue color of the rippled zone the calm streaks are whiter. Studies of calm streaks by Shuleikin (1935 1941), using a somewhat different theoretical approach, yielded similar results.

Particle Motion on the Sea Surface. The hypothesis that calm streaks over internal waves are themselves propagated as waves requires that the material of the surface film shall not follow the steady phase motion of the wave but only the oscillatory horizontal particle motion. It has turned out to be difficult to observe this directly because of inability under natural conditions so to mark the film itself that its motion may be distinguished from that of water lying a few millimeters beneath and from that of objects such as bubbles having some windage profile. Close examination of the upper few millimeters of the sea when a light breeze is blowing shows surprisingly high velocities at the surface and highly developed vertical shear. Thus soluble dye put into the water becomes separated into a subsurface cloud and a superficial film. The film soon vanishes and the subsurface cloud cannot be relied on as a means of observing motion in the very surface. The best targets tried have been sheets of paper that float nearly horizontally just under the surface. These, when placed in front of an on-coming slick, were observed to be drawn into the slick, and, after some minutes, to be ejected to the rear, indicating that the propagation of slicks does not depend directly on surface flow. Nevertheless, up to the present, the conclusion that slick propagation is a wave phenomenon rests chiefly on the evidence of the model experiment.

The Effect of Wind. Only brief mention will be made of observations showing that calm streaks are oriented independently of wind direction at low wind speeds, because sufficient data are lacking to prove this independence categorically. The intuitive notion that slicks trail downwind like smoke from a chimney must be discarded as a *non sequitur* if the initial distribution of film material is uniform. Only some cross circulation of the wind or water, such as that found by Langmuir (1938) and by Woodcock and Wyman (1947), would produce this orientation, and the cases reported by them appear to involve windspeeds in excess of 4 m/sec. At lower wind speeds, downwind orientation is the least frequently observed of any, most tending to be within 30° of perpendicular to the wind. In shallow water, orientaon of slicks is governed by refraction which tends toward parallelism ith the contours of the bottom and of the thermocline, as stated reviously. In deeper water, Forbes (1945) has shown that two trains f slicks can coexist with two different orientations, both of which bviously cannot be related to the local surface wind in the same way. lying across the Gulf of California, the author observed slicks to be riented about normal to the wind direction. It appears, therefore, hat although slicks at low wind speeds are controlled directly by nternal waves, these waves may have some preferred orientation early normal to the wind. In fact Zeilon (1934), by simulating the ondition of a surface current excited by a steady local wind, prouced experimental internal waves with crests at right angles to the vind.

DISCUSSION

Nonperiodic Slicks. Calm streaks on the sea surface are caused by number of agencies other than internal waves. Anything that ompresses the film either by mechanical means or by convergent low will produce this result. Thus a boat sailing through the film plits it into two bands of compressed film that lie on either side of the vake, producing two ribbons of calm in which bubbles are stabilized y the compacted film (Brown, et al., 1949) and which persist much onger than the turbulence of the wake. The attendant drop in surface ension has been measured (Adam, 1937; Shuleikin, 1935, 1941).

Wind stress on the surface produces a zone of calm on the windward ide of a barrier (Aitken, 1884; Adam, 1937; Hardman, 1941). The lischarge of a river into the sea or into an estuary or pool also proluces film accumulation through convergence and hence a calm zone Thompson, 1862; Aitken, 1884; Adam, 1937; Schmidt, 1936).

A commonly observed slick which is not associated with internal vaves forms along the axis or along both sides of tidal channels such as he outer parts of San Diego Harbor or Mission Bay. Similar slicks nave been mentioned by Aitken (1884) and by Schmidt (1936) who ttribute them to the wind, but this explanation is inadequate in everal respects, the most important of which is that they do not isually touch the shore. Preliminary investigation by the author upports the explanation that these channel slicks result from transverse horizontal convergence associated with helicoidal flow along the hannel. Such flow is known to occur in rivers below bends and in iarrow straight channels with sluggish flow (Hellström, 1948; Gibson, A. H., 1909). It is independent of the wind, being caused by friction along boundaries where these are curved or of asymmetric cross ection (Prandtl, 1949; Rouse, 1938: 266–268; Jeffreys, 1929).

In the open ocean, helicoidal flow occurs in the equatorial regio (see Sverdrup, et al, 1946; 632–636, 708–712) and in coastal water (Stockmann, 1946). Since overturn of water is associated with hig biological productivity, it is to be expected that in these regions th surface is heavily contaminated with organic film and consequentl that a slick should be found along the line of horizontal convergenc over that margin of currents which is characterized by subsidence Where a film is considerably compressed, it acts to stabilize bubble (Brown, et al, 1949). Under this condition, a region of convergence i revealed more conspicuously by a line of foam than by a slick. Suc a foam line is a persistent feature off the U. S. Pacific Coast. It ha been photographed and described in detail by Isaacs (1948). similar line of convergence with attendant slicks has been observe and photographed along the left, or "cold wall," of the Gulf Strea (Kielhorn, 1950). Along the (descending) southern margin of th South Pacific Equatorial Current, a line "3 to 4 feet wide, in the for of a long streak of bubbles and foam reaching as far as the eye could se in an east–west direction" was reported by Heard (1950). A simila narrow streak of foam over 100 miles long was photographed an described in detail by Beebe (1926a, b).

Slicks as an Oceanographic Tool. In considering the uses to whic slicks and their relation to internal waves might be put, three stand out First, slicks may be used to locate regions of horizontal convergence a the sea surface. Second, internal wave slicks represent a map of th distribution of the internal waves and so lend themselves to study o the conditions under which such waves are formed. Third, the fac that at wind speeds greater than 3.4 m/sec the film is dominated b the wind rather than by the motion of the underlying water may she new light on quantitative aspects of the stress of wind on water.

Inhibition vs. Damping of Ripples. In closing, it is worth pointin out that the calming effect of film on water has been attributed herei solely to variation in the rate at which ripples, once generated, ar damped by viscosity of the water. The possible effect of the film o the tangential stress of wind on water has been ignored on the supposition that this is relatively unimportant. It must not be overlooked however, that careful observations have been reported (Aitken, 1884 Gibson, G. E., 1944) which indicate that the wind-induced surfac current is increased by the presence of oil on water. Aitken ha suggested that, by distributing the effect of stress from small eddie over areas which are large compared to the length of initially forme ripples, an elastic film discourages the irregular horizontal motion o the water surface which initiates ripple formation, favoring instead iform surface drift. These matters deserve further study. Should turn out that such variation in the action of wind on water may leed be induced by surface film, the effects on rippling due to damp- would in no way be diminished; on the contrary they would be pplemented.

CONCLUSIONS

1. The surface of coastal waters and of lakes is often coated with n of finely particulate or colloidal material, rich in organic matter.

2. Such films, when in a compact state, lower the surface tension in oportion to the degree of compaction. They therefore make the ter surface elastic and increase the rate of dissipation of wave ergy for wavelengths from a fraction of a millimeter to several eters. This increase more than doubles the minimum wind velocity quired for the growth of waves.

3. Long internal waves in a shallow thermocline produce transient anges of state in a surface film sufficient to form bands of variable rface tension over their troughs. These bands are propagated as a ve with the same velocity as the internal wave.

4. Provided the internal wave be of sufficient amplitude in relation its depth, light winds (less than Beaufort 3) render the bands sible as long narrow calm streaks in a rippled sea.

5. At wind forces less than 3, internal waves of short period in a allow thermocline are usually oriented with their long axes nearly rpendicular to the wind except in shallow water where they are fracted by the thermocline or bottom to an orientation nearly rallel to the contours of one or the other of these surfaces.

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actions, American Geophysical Union   Volume 32, Number 1   February 1951

TOTAL REFLECTION OF SURFACE WAVES BY DEEP WATER

John D. Isaacs, E. Allan Williams, and Carl Eckart

(Contribution from the Scripps Institution of Oceanography, New Series, No. 498)

Abstract--A mechanism is described by which surface gravity waves generated in iallow water may be totally reflected from deep water. The mechanism by which waves enerated in deep water may be "captured" is also discussed.

itroduction--It has been the intuitive feeling of those engaged in the studies of shoreline pros that some mechanism must exist by which the surf zone can resonate to the fluctuations in ight of the wind waves and swell. These fluctuations have been observed to produce variain the average height of the water line, and recently have been described and named "surf " [MUNK, 1949]. The phenomenon which has required the assumption of a resonant system t the fluctuations in average water level bear no simple relationship to the momentary height wave groups and are much affected by the periodicity of their occurrence. The surging of irf zone displays a beat phenomenon, successively being in and out of phase with the incomroups. This beating frequently results in a period of exaggerated surging followed by a per- low surging, both coinciding with the arrival of similar groups of high waves. Also there netimes no conspicuous surging, and on other occasions almost continuous surging. It is sted that these differences depend upon the relation of the resonant period to that of the ing waves.

'o the observer these have always suggested the forced oscillation of a resonant system, but iow no mechanism has been described that would explain resonant periods of the water over ping bottom of infinite seaward extent. Such a mechanism is suggested below. This mechaalso has other important applications to the problems of shoreline processes.

'otal reflection of surface waves by deep water--Consider a straight beach with parallel con-, so that the phase velocity C of surface waves is a function only of the distance, y, measured ndicular to the shore. Then, if α is the angle between a ray and the y-axis, Snell's law states in α/C = constant, along the ray. If C_0 is the deep-water velocity, and α_0 the angle of aph from deep water, the equation becomes

$$\sin \alpha = (C/C_0) \sin \alpha_0$$

α and C refer to some value of y.

'onsider how α varies with α_0. The maximum value of $\sin \alpha_0$ is unity, and this occurs for s that, in deep water, are propagated parallel to the beach, that is, glancing incidence. For waves, $\alpha = \alpha_c$ where the critical angle α_c is given by

$$\sin \alpha_c = C/C_0$$

all waves generated at sea pass across the contour at distance y at an angle less than this al value.

lowever, waves may be generated in shallow water with angles greater than α_c. Such waves ot be able to reach deep water, but will be totally reflected, at that depth where the wave ve- is C_m, given by

$$C_m = C/\sin \alpha, \quad \alpha > \alpha_c$$

is illustrated in Figure 1, which shows how a ray that leaves shallow water at an angle greatin α_c is curved and returns to the beach after having been deflected parallel to the beach at stance y_m from shore.

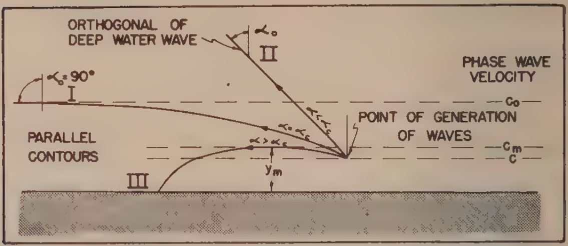

ORTHOGONAL OF
DEEP WATER WAVE
α_o
II
$\alpha_o = 90°$
I
PHASE WAVE
VELOCITY
C_o
POINT OF GENERATION
OF WAVES
$\alpha_o < \alpha_c$
$\alpha > \alpha_c$
PARALLEL
CONTOURS
C_m
C
y_m
III

Fig. 1--Waves generated in shallow water and refracted over parallel straight contours; I, orthogonal of wave generated in shallow water with the critical angle α_c enters deep water at an angle α_0 of 90°; II, orthogonal with $\alpha < \alpha_c$; III, wave generated in shallow water with angle $\alpha > \alpha_c$ is reflected from deep water at depth y_m

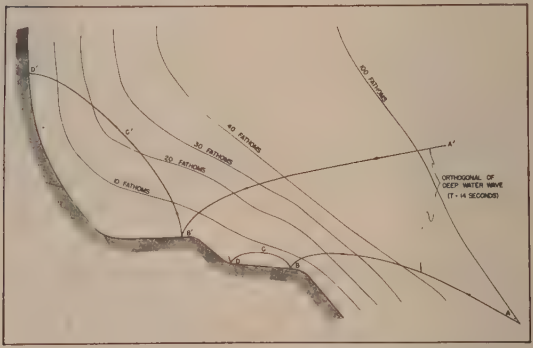

D′
C′
100 FATHOMS
40 FATHOMS
30 FATHOMS
20 FATHOMS
10 FATHOMS
A′
ORTHOGONAL OF
DEEP WATER WAVE
(T = 14 SECONDS)
B′
C
D
B
A

Fig. 2--Total reflection from deep water occurs at C or C′ for waves generated in deep water and reflected from a curved beach

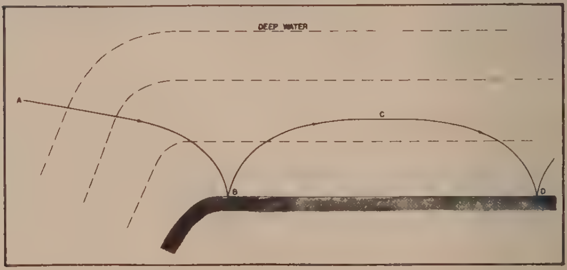

DEEP WATER
A
C
B
D

Fig. 3--Deep water wave, which enters shallow water over curved ontours and crosses straight contours at an angle greater than the critical angle, is reflected from the shore at B and totally reflected from deep water at C

Consequently one may expect the formation of standing waves, reflected alternately fr
beach and from deeper water. These standing waves will have natural periods, much as th
ing waves in an organ pipe are responsible for its resonance. However, in general the natu
quencies of a sloping beach will not be integral multiples of a fundamental, as is the case w
organ pipe or stretched string. Nonetheless, they will be resonance frequencies, so that a
tively small exciting force of proper period can produce relatively large effects.

The process of total reflection from deep water can also occur on curved beaches, fo

ated in deep water and reflected from the beach. This is shown in Figures 2 and 3. Waves
ated at sea come into shore along the curved ray AB, are reflected by the beach at B, and
ed along the ray BCD, being totally reflected at C.

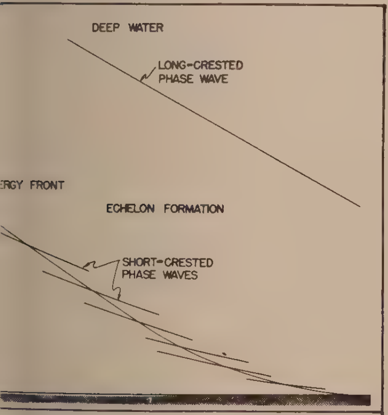
he reflection at B is complicated by surf and breaker phenomena for waves of ordinary per-
nd heights, so that the coefficient of reflection at B may be very small. For very low ampli-
vaves, however, the coefficient of reflection at the beach may be nearly unity. This low am-
e may be caused by the initial refraction along the ray AB. Breakwaters and jetties may al-
lect waves in such a manner that they are totally reflected and returned to the beach from
water.

nother topographic situation that may make for total reflection from deep water is a bar
ed by shallow water. Waves generated over the bar will be reflected from the deep water
h sides. Similarly wind waves generated in a shallow sea, such as the Bering Sea, may be
ted from adjacent deeper seas. Total reflection can also occur from regions of variable
nt.

eneration of waves in shallow water--The generation of wind waves in shallow water has al-
been mentioned but there are other possibilities.

he generation of waves with periods of several minutes (surf beat) by groups of breakers
een discussed by MUNK [1949]. Whether such waves move out to sea, or are totally reflected
eturn to the beach, depends on the angle of their front to the bottom contours. This question
een investigated, using methods similar to those employed by STONELEY [1935] in treating
fraction of groups of incoming waves.

a group of long-crested waves advances from deep to shallow water, the effect of refrac-
ill be to convert it into a group of short-crested waves, advancing toward shore in an ech-
ormation (see Fig. 4). The diagram is, of course, exaggerated, since even deep water waves
have crests that are indefinitely long. A detailed investigation of several possible cases of
s of long-crested waves approaching shore at an angle, shows that the surf-beat wave gen-
l by an echelon of waves will be totally reflected by the offshore waters. Hence one may al-
ect the surf beat to consist of standing waves, reflected alternately from the beach and from
water, as was suggested above.



4--Echelon formation of short-crested
ves produced by group refraction

The seiches revealed by tide records at exposed locations and sometimes attributed to the resonance of "offshore basins" and similar topographic features are probably merely an example of the multiple reflection of long period waves between the shore and the deeper water, and may be only slightly affected by the bottom topography in deeper water.

This effect, combined with reflections from headlands, very likely accounts for the surging of open harbors like Monterey Harbor. The force exciting these surges may be the surf beat on adjacent beaches.

There have been observed very high amplitude surges with periods of several minutes on perfectly open coasts [MUNK, 1949]. The forces causing these surges are not obvious, although they must be connected with heavy seas. As a working hypothesis, one may assume that the resonance due to the sloping bottom is an important factor.

cknowledgment--This work represents results of research carried out for the Beach Erosion
, Corps of Engineers, Department of the Army, Contract W-49-055-eng-3.

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(Communicated manuscript received July 24, 1950; open for formal discussion until July 1,

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PHOTOGRAPHY RELATED TO INVESTIGATION OF SHORE PROCESSES

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Reprinted from
PHOTOGRAMMETRIC ENGINEERING
December
1950

PHOTOGRAPHY RELATED TO INVESTIGATION OF SHORE PROCESSES*

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INTRODUCTION

THERE are many ways in which photographs can be used to assist in the study of shore processes and in tracing the history of shoreline development. Storm waves cause important changes to shorelines. The observer finds it difficult to determine the nature of the wave attack because of the rapid and confused motion, but photographs allow more leisurely examination of the wave character. Furthermore, photographs obtained before and after storms show graphically the changes which beaches have undergone. The retreat of coastal cliffs can often be determined by a comparison of the present cliffs with old photographs. The camera is particularly useful in conveying to others the special phenomena which an investigator finds on beaches. A photograph is usually more convincing than a sketch although both are needed to some extent.

Photographs from planes are essential in order to show the larger features which are badly foreshortened by photographs from the land surface. Currents are often indicated by a difference in transparency of the water. Taken from the land, these differences scarcely show; but they are strikingly clear when viewed from the air. Where the water along the shore is clear, aerial photographs serve to indicate channels and bars which exist along the shore in many places. Finally, the airplane is capable of making aerial compilations which produce the most accurate types of shoreline maps.

WAVE PHOTOS

Waves can be photographed to best advantage from piers where the waves pass beneath the photographer, or from cliffs against which the waves are breaking. Where large waves are breaking on a gently sloping foreshore, photographs from the beach are generally disappointing unless telephoto lenses are used.

There are two types of breakers which result from wind waves, spilling and plunging. These are illustrated in Figures 1 and 2 respectively. Although both types have steep fronts, the spilling breaker lacks the almost vertical fall of the water that characterizes the front of a plunging breaker. Spilling breakers are characteristic of waves which are breaking with strong onshore wind in storm areas. Plunging breakers occur where waves have far outrun the area of storm generation, and are particularly pronounced when there is an offshore wind. Waves are likely to spill if they move in along a gently sloping beach, and the same waves will plunge if they encounter a steep foreshore. All gradations exist between the two types.

Tsunamis (popularly known as tidal waves) are not unlike ordinary wind waves in appearance along the shore (Figures 3 and 4) partly because they usually have wind waves superimposed on top of them. Actually they are very different in their open sea characteristics because they have very low heights in the open ocean and occur at intervals or periods of from about 10 to 20

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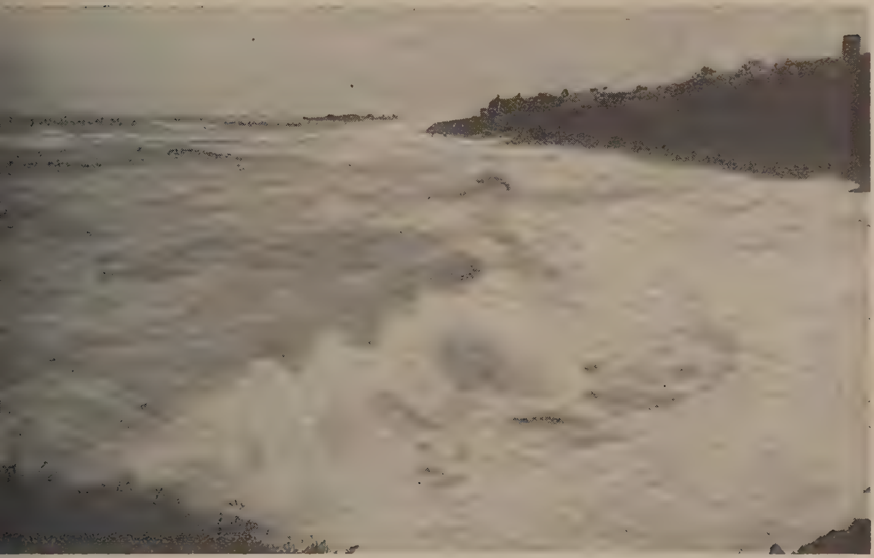
* Contribution from Scripps Institution of Oceanography, New Series No. 499. This work represents in part the results of research carried out for the Office of Naval Research and the Beach Erosion Board under contract with the University of California.



1. A spilling breaker taken during a gale at Marblehead Neck, Mass., September 12, 1950.

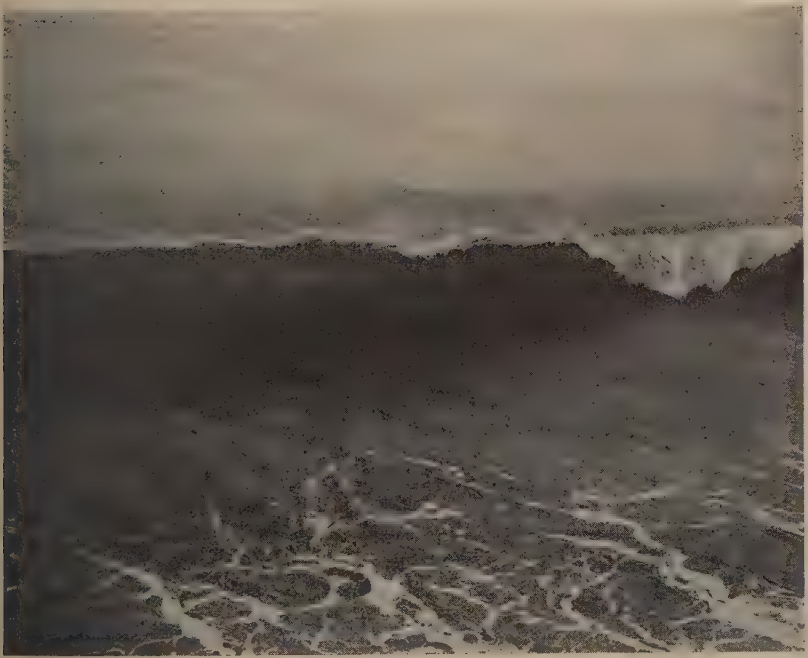


FIG. 2. A plunging breaker at La Jolla, Calif. Note the apparent concavity of the wave front in the portion which has not yet broken.

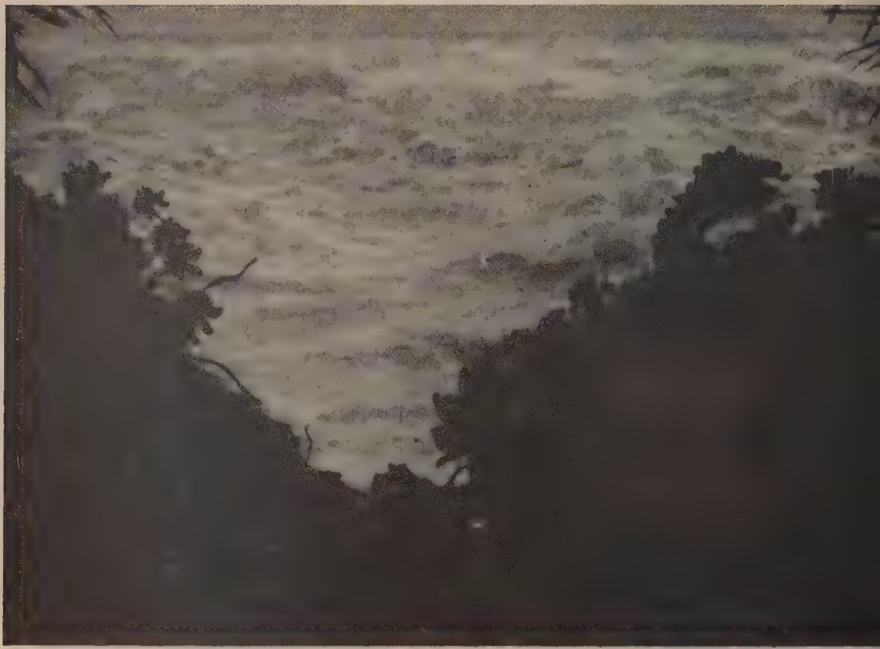


FIG. 3. The tsunami (tidal wave) of April 1, 1946, at Kawelo Bay, Oahu. The advancing wave crossing a lagoon inside a coral reef. It covered the entire foreground a few seconds later.

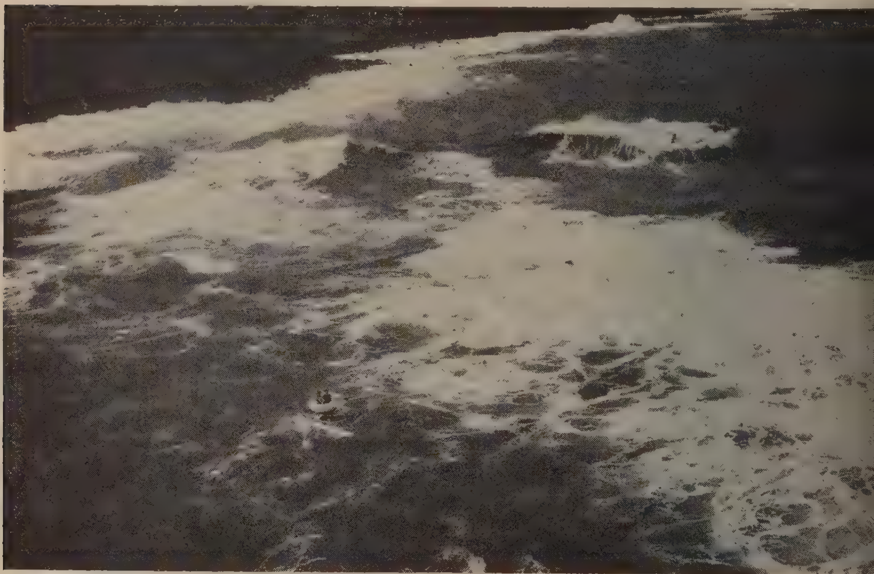


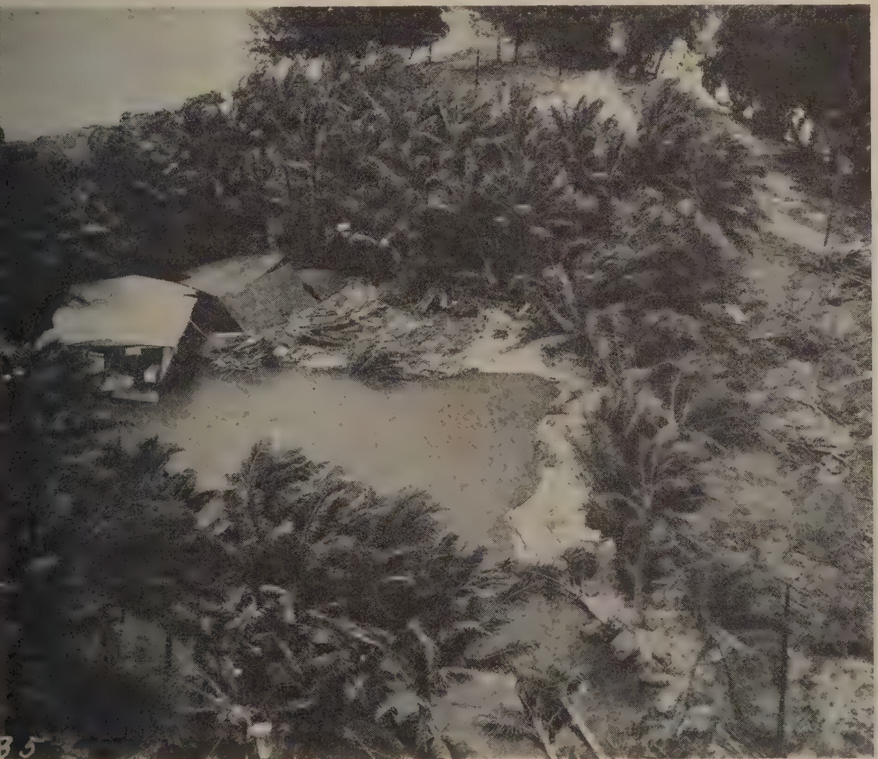
FIG. 4. Photograph taken by the U. S. Navy during the same series of waves illustrated in Fi ure 3. The people on the life raft had been swept off Laupahoehoe Peninsula in Hawaii and we rescued by U. S. Navy fliers who dropped them a raft. The photograph was apparently taken duri the rise of one of the waves onto the coast.

inutes whereas wind waves have periods from about 2 to 20 seconds. Along iores tsunamis rise to great heights, this rise being much faster than but ten similar to the rise of the tide. The piling up of the water to great heights roduces extensive damage often carrying away houses like those shown in igure 5. The advantage of taking photographs during a tsunami can be well nagined since the excitement of the moment makes it most difficult to recall cactly what was happening especially where the wave is coming directly at ne as was the case in the photograph which the author obtained in 1946 Figure 3).

The variability of wind wave height along the shore is well illustrated by lane photographs (Figure 6). The differences are generally the result of con- ergence and divergence of trains of waves approaching the coast. In Figure 6 ne almost complete absence of breakers in one area is the result of a divergence used by the existence of a submarine canyon on the sea floor.

RIP CURRENTS

"The undertow is dangerous on this beach" is a common but meaningless atement. It can be translated into actual demonstrable fact by saying "There e strong offshore currents along this beach." Undertow as a strong subsurface urrent is probably a rare phenomenon, but strong currents which carry bathers ut from the shore either at the surface or below are by no means unusual in



IG. 5. Photograph by U. S. Navy of a portion of Kawelo Bay after the large waves of April 1, 1946, showing how two houses were washed into a small sink hole lake and completely demolished.

high surf. These outward moving currents are known locally as *rip tides* or *pusses*, but the name *rip currents* seems preferable especially since the phenon non has no relation to the tide, and the origin of *sea pusses* is a bit uncerta possibly originating as *sea purse.*

The roiled water in the rip currents gives them a distinctive appearar which can be seen best from an elevation. An airplane photograph (Figure is particularly helpful in showing the nature of these currents. They are gen ally concentrated into a narrow band as they move out through the breake

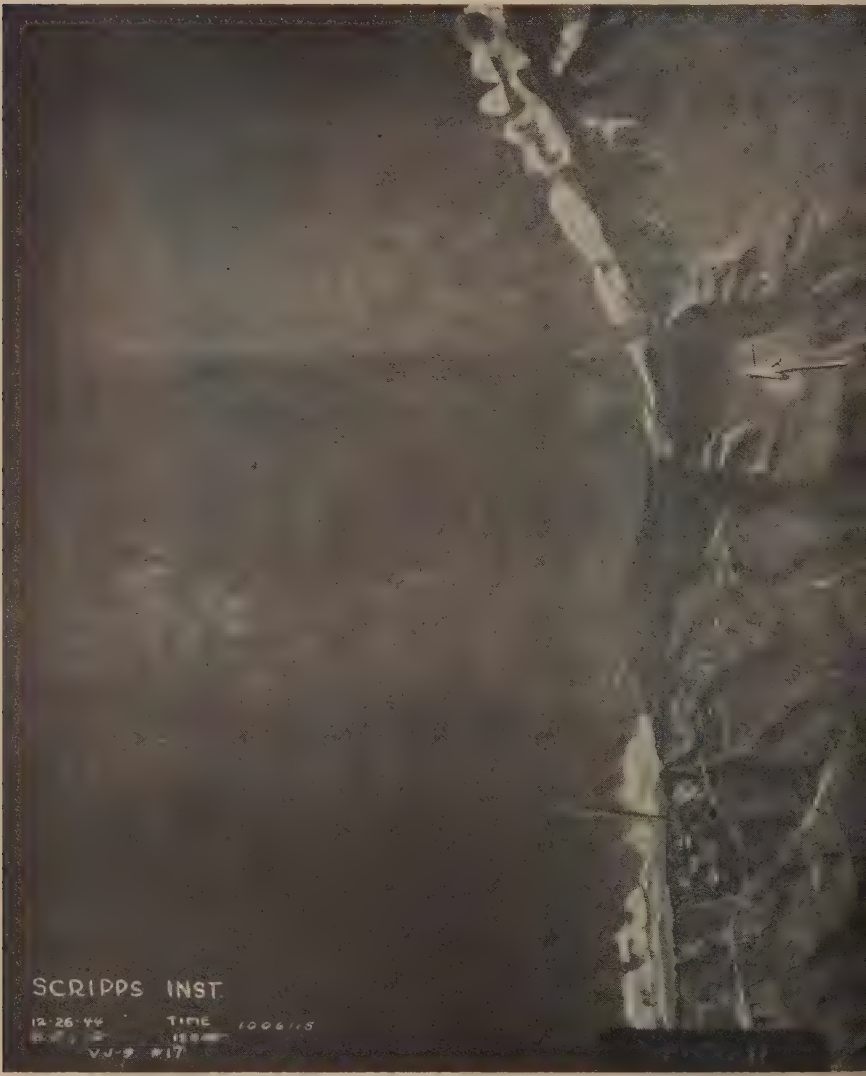


FIG. 6. Illustration of the effect of a submarine canyon (located outside the arrow) in reduc breaker height. Note that the surf zone which is well developed on both sides virtually disappe in this zone. Photo by U. S. Navy, 1944.

ut become diffused on the outside and often take on the form of large eddies. Vhere waves are breaking against rock cliffs, masses of foam develop. The utward movement of rip currents carries the foam seaward in lines as indicated n Figure 8.

The movement of muddy water out over the sea surface is very evident after large rain storm. This is the result of the lower salinity of the water from the and which is entering the ocean. The water may move out very much like a ip current. Similar phenomena are seen off rivers which empty directly into he sea. In the case of rivers like the Amazon, these muddy top flows can be raced for hundreds of miles out to sea. A marked color contrast exists at the oundary between the murky water and the clear water beyond.

BEACH PHENOMENA

In *Douglas Johnson's* "Shore Processes and Shoreline Development," a onsiderable number of photographs were used to illustrate the special features

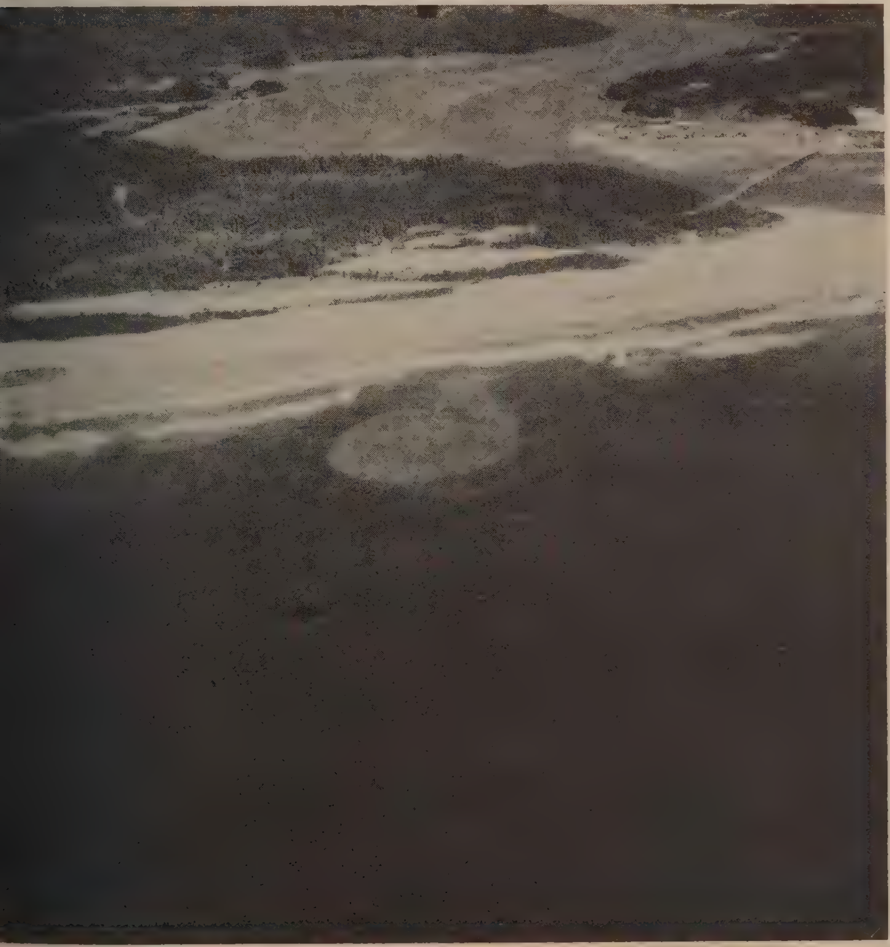


FIG. 7. Aerial photograph by J. D. Isaacs showing a rip current moving out from the Oregon coast in a zone of reduced breakers. Note the eddy in the expanding outer portion of the rip.

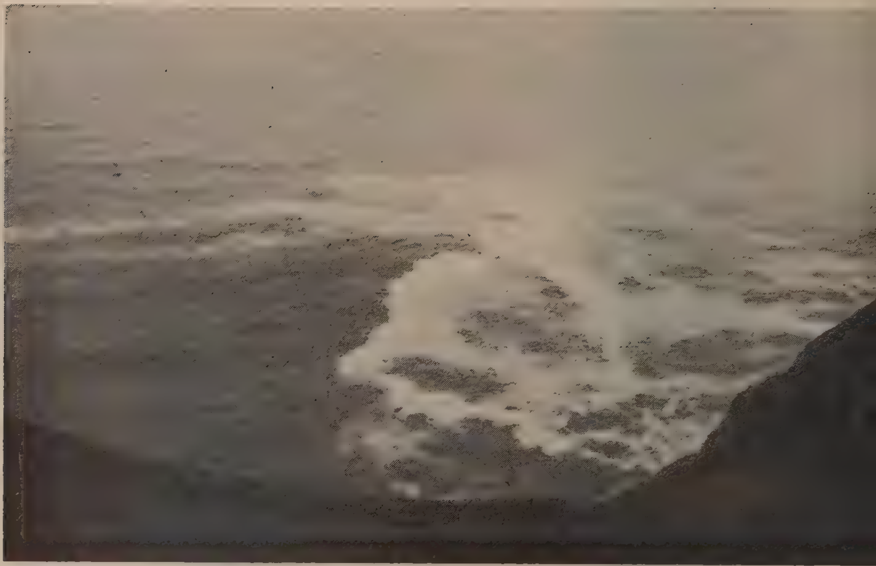


FIG. 8. A rip current carrying masses of foam out to sea. Photograph taken from the Oregon Coast Highway at Sea Lion Cave, June 16, 1950.

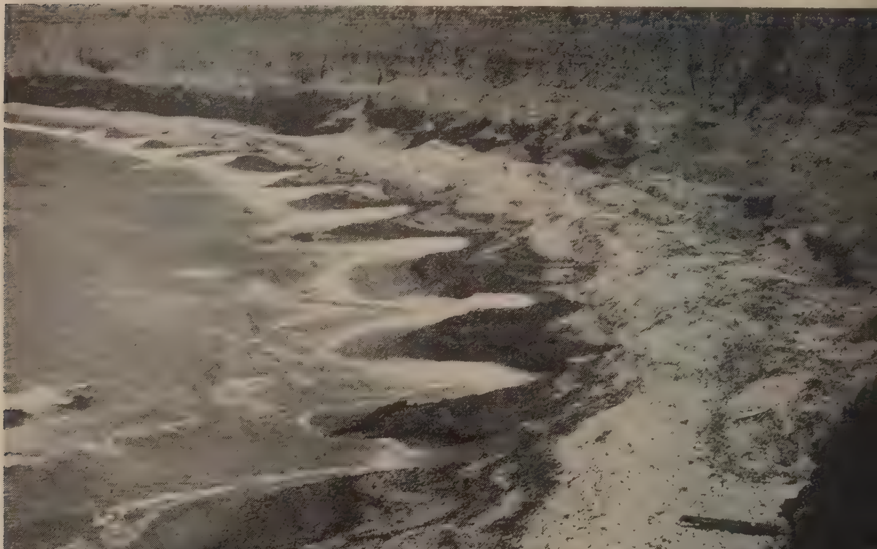


FIG. 9. Beach cusps formed from cobbles at Punta China, Lower California. Note the backwash in the troughs between the cusps. Photographed August 6, 1950.

beaches. Study of these same features has continued and new phenomena ve been discovered which lend themselves to photography.

Beach cusps are often developed in sand but they are most striking in cobble aches (Figure 9). The photographs show how the small ravines between cusps e kept open by the concentration of the backwash in the initial depressions. rplane photographs give indications of the relation between cusps, beach nds, and angles of wave approach.

The longshore bars and troughs which are commonly developed where aches have gentle seaward slopes are partially exposed at low tide. Photoaphs show the effects of strong currents which have been flowing at high tide ong the troughs and have left striking irregularities (Figure 10). In places air otos show the bars and troughs through the clear water (Figure 11).

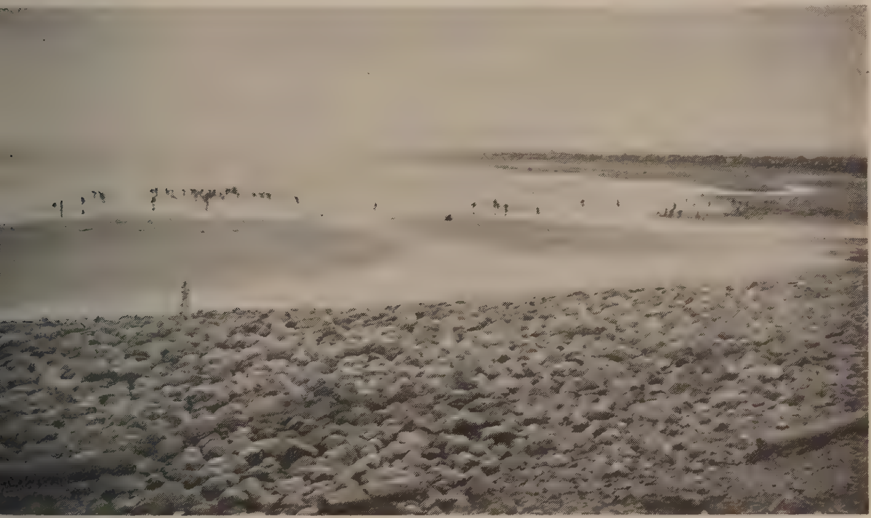


FIG. 10. An early morning low tide at Seaside, Oregon, June 17, 1950. Clam diggers are working the exposed longshore bars. Note the longshore trough in the middle ground and the seaward nnections through the bar formed by rip currents at higher stages of the tide.

A great variety of ripple marks develop on beaches and on their submerged ntinuations. The development of *backwash ripples*, characteristic of fine sand aches with gentle seaward slopes, is illustrated in Figure 12. These ripples e almost always separated by one to two feet, whereas ripples of about 3 inch ave length are found in the submerged slope directly outside. Sometimes at w tide one set is found superimposed on the other, but ordinarily the short pples disappear as the water withdraws and longer ripples are formed by the ckwash.

BEACH CYCLES

During the summer season, when small waves prevail in most areas, the aches grow broader and the sand piles higher. During winter storms, however, e beaches are likely to be denuded. These changes are illustrated in Figure 13. owever, the changes may be partly in the nature of sand shifting along the ore. Figure 14 shows a beach which grows in summer at the north end beuse the waves are approaching from the south, whereas the south end of the me beach is actually denuded during the same period. When winter storms

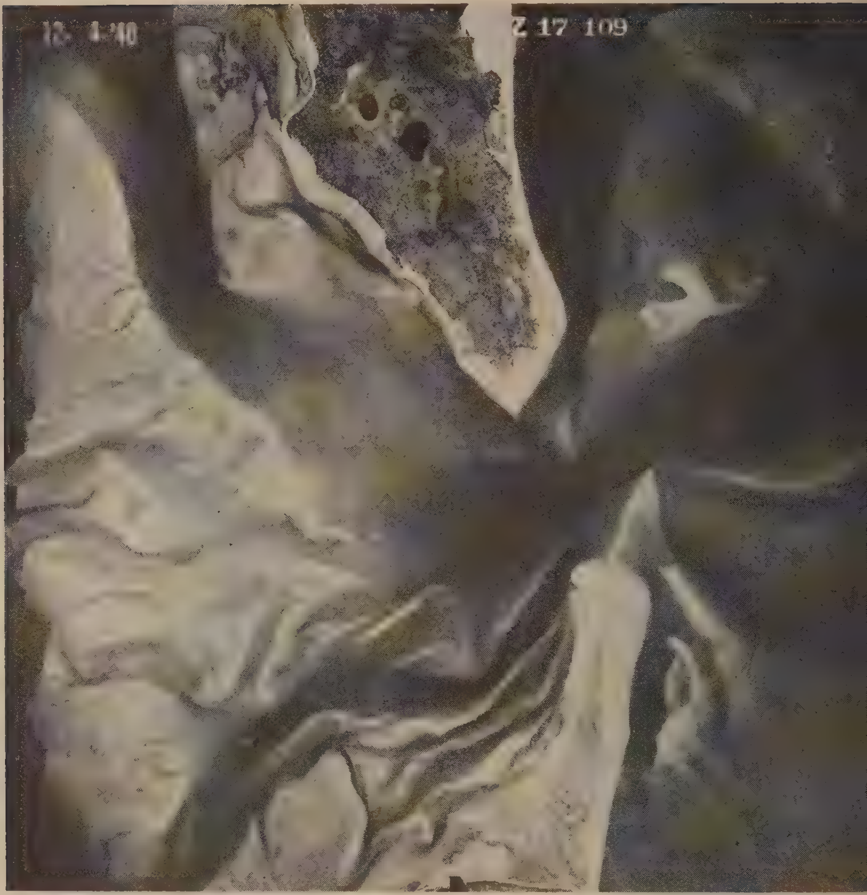


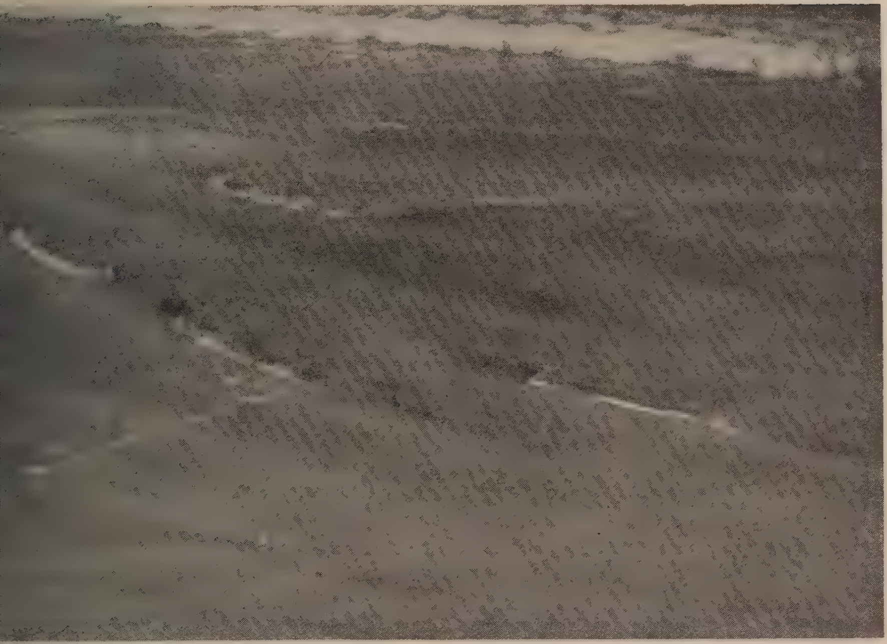
FIG. 11. Aerial photograph by Gulf Oil Company on the coast of Mozambique, Africa, kinc
supplied to the author by Dr. H. D. Hedberg. Note the troughs and bars along the coast and t
intricate tidal channels on the inside. Unusually clear water made this submarine photograp
possible.

come in from the northwest, the northern portion of the beach is cut down
rock, whereas the southern portion receives a sand cover, although there is
actual loss of total sand on the entire beach.

Photography of beaches after large storms shows that in general the larg
waves straighten the slope cutting away the flat berm, but piling up the san
at the inner margin of the beach and to some extent building up the low
beach.

COAST EROSION

In some areas it is possible to tell the extent to which a coastal cliff has r
treated during historical times, by the use of old maps which show how portio
of towns have been worn away due to the attack of the waves. In general, hov
ever, little information is available to indicate what has happened to coas
since man inhabited them. Photography is of some assistance. Fortunately, th
shore has been a popular place to take photographs. This gives us a possib



IG. 12. Formation of backwash ripples by the backflow of a wave moving seaward down a fine sand beach. Photograph by R. L. Wisner at Mission Beach, California, July 14, 1947.

heck over a period of about one century. There are often enough buildings still emaining to give some notion of retreat. In the case of rock coasts, if erosion as been very slow, concretions or other special features of the rock face can be ecognized in the old photographs. An example of very small erosion indicated y the presence of the same concretions after an interval of 42 years is shown in igure 15. It is surprising how many similar cases of little change can be found n coasts where wave attack is relatively violent. On the other hand significant hanges seem to be common on rocky coasts where arches or stacks stood out eyond the general trend of the coast. Such a case is illustrated in Figure 16. he disappearance of sea arches has often served to give the impression to local nhabitants that coasts are retreating far faster than is actually the case.

The difficulty of getting dates for old photographs should convince photog-aphers of the importance of dating their present day films. The help to future eologists of such dating may be tremendous.

(*The remaining figures are shown on the following pages*)

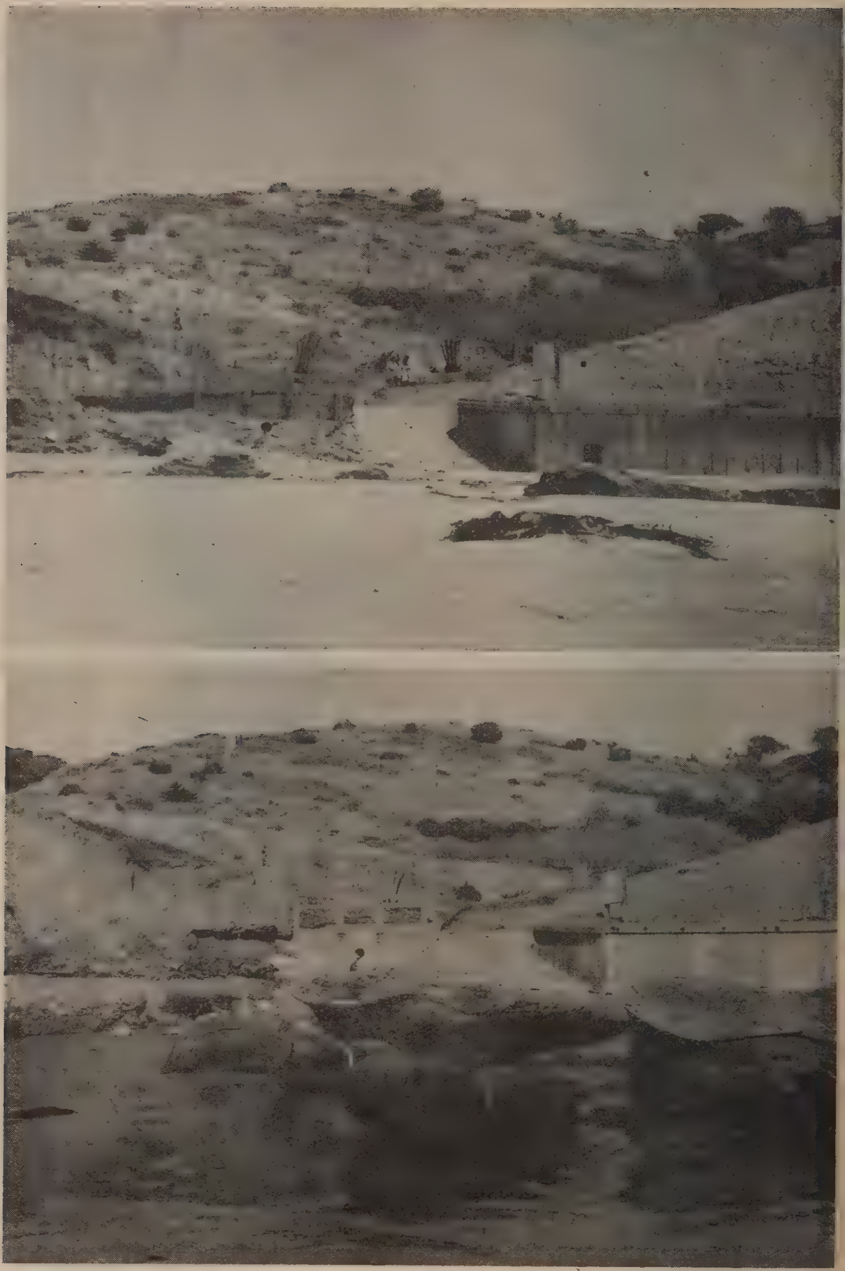


FIG. 13. Filled state of the beach (upper view) at Scripps Institution in August, 1938, a (lower view) the cut state in March 1938. Note that the rocks are almost entirely covered in t upper photograph.

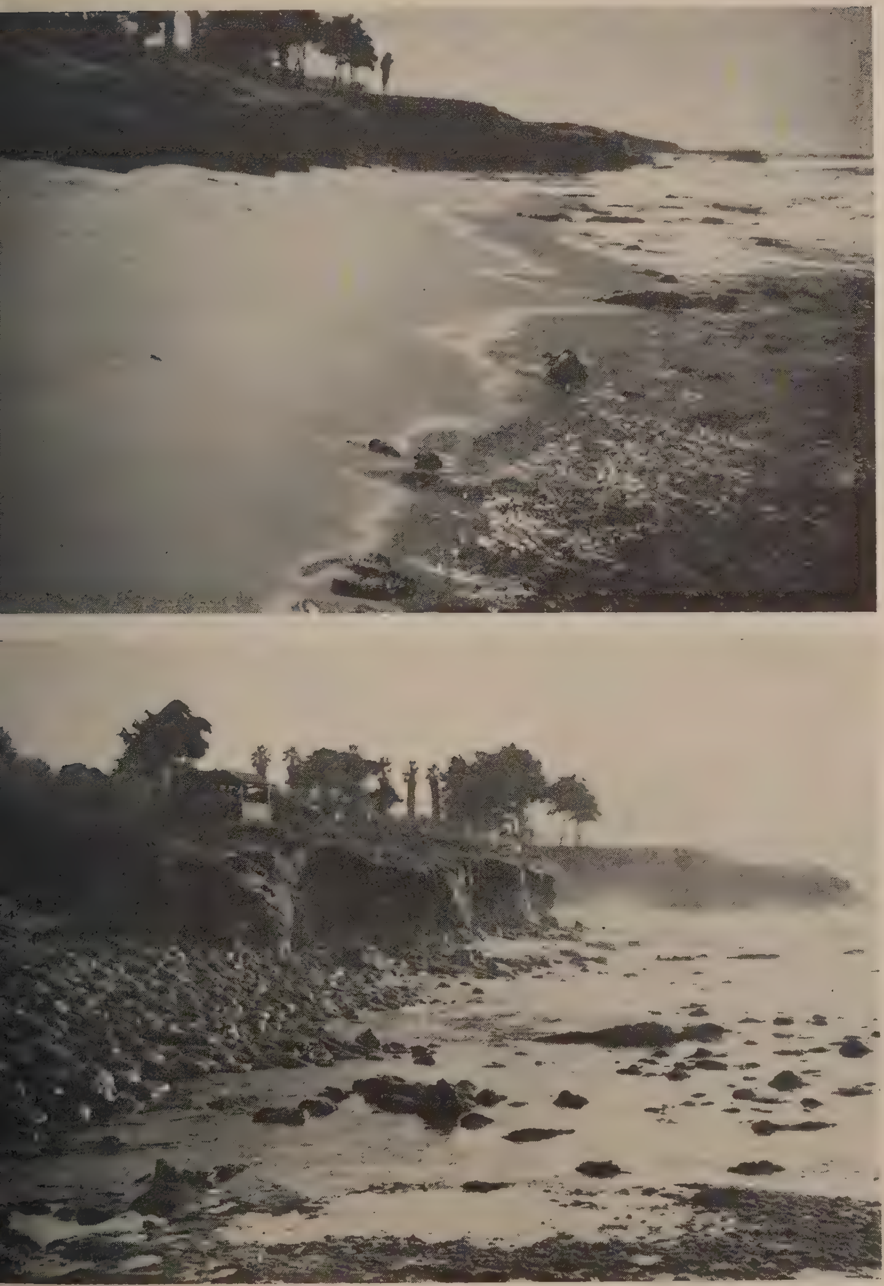


FIG. 14. Illustration of the shifting of sand from one end to the other of a pocket beach at a Jolla, California. The upper view was taken in September, 1948 after a period of waves with southrly approach had moved the sand towards the rocks on which the photographer stood. The lower iew of the same locality shows the denuded beach in November, 1947 after a period of northresterly approaching waves. Careful examination will show that there has been some growth of the each in the background.

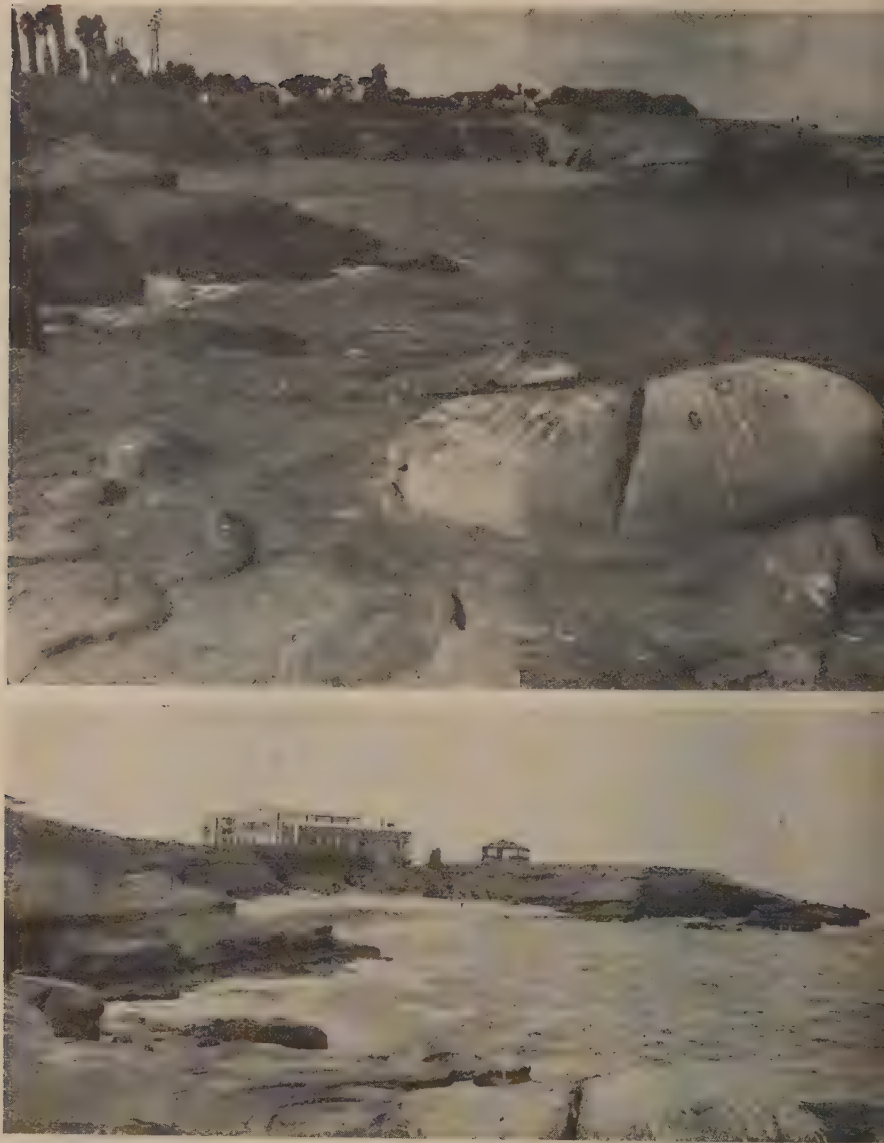


FIG. 15. The absence of appreciable erosion of the sandstone cliffs at La Jolla, California during an interval of 42 years. The upper photograph was taken in 1948 by *U. S. Grant IV* and th lower one in 1906. Note the large number of common concretions that can be identified in bot photographs.

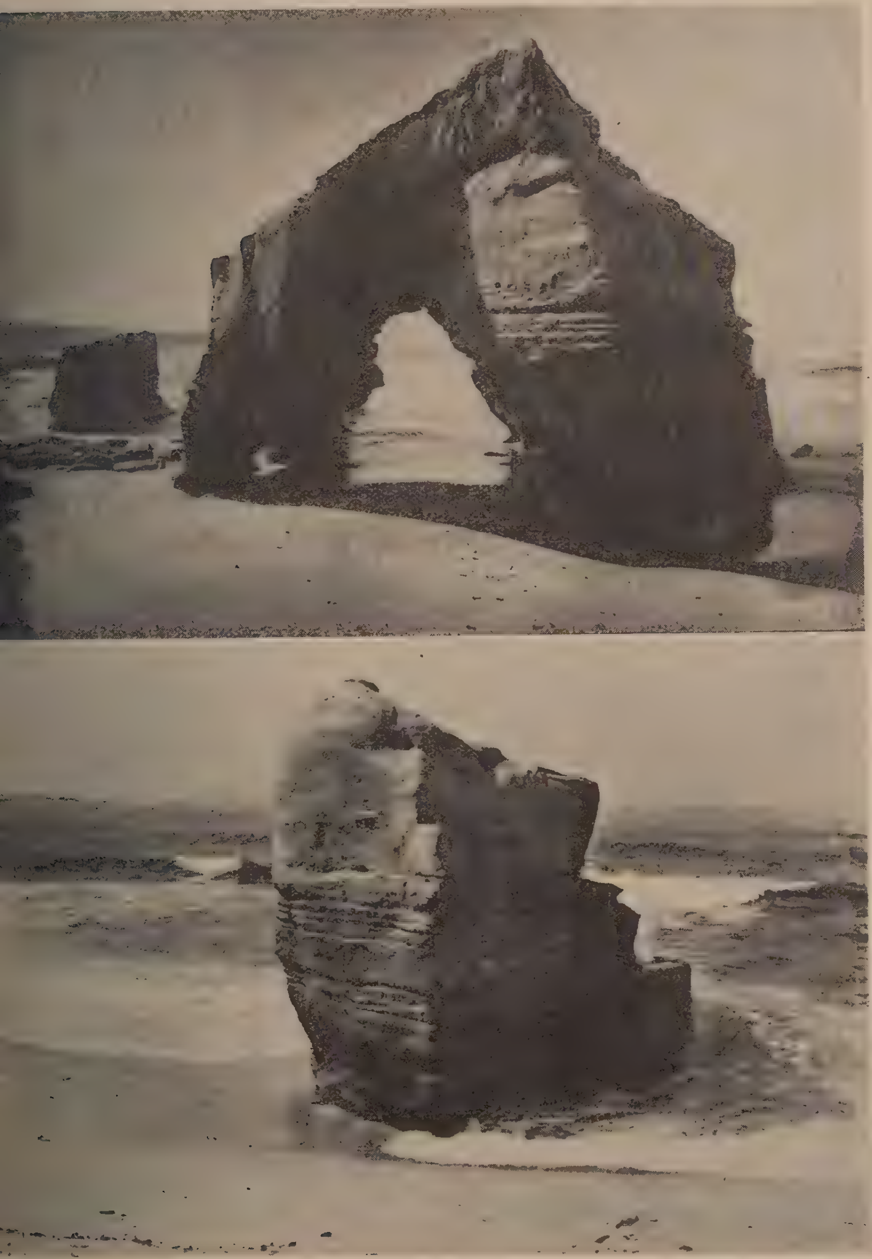


FIG. 16. Cathedral Arch at La Jolla, California, which was destroyed about 1900. The upper otograph was taken in 1897, and the lower one was taken in 1945 by *U. S. Grant IV*. The lower otograph shows the remaining right buttress of the arch. The other portions have completely sappeared.

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NUMBER 530 MARCH 14, 1951

OCCASIONAL PAPERS OF THE MUSEUM OF ZOOLOGY

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NOTROPIS AMNIS, A NEW CYPRINID FISH OF THE MISSISSIPPI FAUNA, WITH TWO SUBSPECIES[1]

BY CARL L. HUBBS

Submitted for publication April 27, 1950

RECENT exploration of the rich cyprinid fish fauna of eastern North America, accelerating through the past quarter century, has revealed and is continuing to reveal new species referable to the dominant genus *Notropis*. One of these is a small species that has been called *Notropis amnis*, though it has never been assigned an available name. It is the purpose of this paper to propose this name formally, to diagnose the 2 subspecies into which it is divisible, to summarize and clarify their confused nomenclatorial history, to discuss their intergradation, and to map and interpret their geographical distribution.

Most of the material on which this paper is based is deposited in the University of Michigan Museum of Zoology (U.M.M.Z.) and the United States National Museum (U.S.N.M.). Use has also been made of the specimens in the collections of the Illinois Natural History Survey, the University of Wisconsin, Indiana University, the University of Texas, the Oklahoma Agricultural and Mechanical College, the Agricultural and Mechanical College of Texas, and the Upper Mississippi River Survey Committee.

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[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 500.

George S. Myers and later Leonard P. Schultz, as the curators of fishes at the National Museum, and Reeve M. Bailey, my successor at the University of Michigan Museum, have accorded every facility in this and other studies. Bailey, further, has contributed helpful suggestions during the preparation of the manuscript. Schultz, with the aid of Clarence M. Tarzwell, collected most of the types of *N. a. amnis.* For specimens and records or for laboratory assistance, I have thanks to express to other associates and former students, including John D. Black, Shelby D. Gerking, John T. Greenbank, George V. Harry, Clark Hubbs, Raymond E. Johnson, Chancey Juday, Canuto G. Manuel, George A. Moore, D. John O'Donnell, I. A. Rodeheffer, Philip W. Smith, Laurence C. Stuart, and George W. Wagner. Especial thanks are due C. Willard Greene, who collaborated in the discovery and definition of *N. a. amnis,* and Kelshaw Bonham, who, similarly, collaborated in the recognition of *N. a. pinnosa* and, in addition, made the many measurements and scale counts that are summarized in Table IV and took the photographs that are reproduced as Plate I. Laura C. Hubbs aided materially in processing the data, in spot-mapping the distributional records, and in other ways. Kirby H. Walker provided data on the habitat of *N. atrocaudalis.*

PALLID SHINER

Notropis amnis Hubbs and Greene, new species

Notropis nocomis (2 species originally confused; diagnosis refers to a subspecies of *N. volucella*).—Jordan, 1885: 812 (24, sep.) (ascribed to "Jordan & Gilbert, 1885," without trace of description^{P}; fresh water, Southwest^{P}). Evermann, 1892: 78–79 (original description as "sp. nov."^{P}; Trinity River at Magnolia Point and Buffalo Bayou near Houston, Texas^{P}). Evermann and Kendall, 1894: 83, 89, 91, 100, 126, Pl. 17, middle fig. (Rio Comal at New Braunfels [in small part], Trinity River at Magnolia Point, Trinity River at Dallas [in part], Texas^{P}). Jordan and Evermann, 1896*a:* 268 (description^{P}; records and range, in part [after Evermann and Kendall^{P}]; locally abundant^{P}); 1896*b:* 253 (listed, same localities^{P}); 1900: 3241, Pl. 17, Fig. 118^{P}. Pratt, 1923: 78 (diagnosis^{P}; same localities^{P}).

Hybopsis nocomis.—Jordan, 1929: 78 (diagnosis^{P}; range, St. Louis^{A} to Texas^{P}). Jordan, Evermann, and Clark, 1930: 135 (records and range, in part [after Evermann and Kendall]^{P}). Pratt, 1935: 74 (same as Pratt, 1923: 78^{P}).

Notropis deliciosus (misidentification).—Jordan and Gilbert, 1886: 23–24 (Comal River at New Braunfels, Texas, in small part^{P}). Evermann and Kendall, 1894: 80, 91, 100 (Jordan and Gilbert's record^{P}).

[*Notropis*, species] "closely resembling *N. cayuga*."—Jordan, 1891: 18 (characters^{P}; Rio Comal at New Braunfels, Texas^{P}).

Notropis cayuga (misidentifications).—Meek, 1896: 347 (Old River at Buckhorn Landing near Greenway, Arkansas^{I}; scarce^{I}). Jordan and Evermann, 1896*a*: 260 (Arkansas record only^{I}). Forbes, 1909: 386 (range, in part, "Lower Miss^{I}. and Ohio"). Forbes and Richardson, 1909 and ed. 2, 1920: lxxvii, 133 (range in part^{I}; Arkansas and lower Mississippi Valley [both presumably based on Meek's record, also included under *N. c. atrocaudalis*]^{I}; Comal River^{P} [in part; Neches River cited with no obvious basis], Texas). Thompson and Hunt, 1930: 24, 43, 98 (characters in key, habitat, and nomenclature, in part^{A}; Champaign County, Illinois^{A}).

Notropis cayuga atrocaudalis (misidentifications).—Forbes, 1909: 386 (range in part, "Lower Miss^{I}. and Ohio"). Forbes and Richardson, 1909 and ed. 2, 1920: lxxvii, 134 ("Lower Miss^{I}. and Ohio"; Greenway, Arkansas^{I}). Thompson and Hunt, 1930: 24 (subspecies identification of form otherwise treated as "*Notropis cayuga*," revised to *N. heterolepis*^{A}; habitat^{A}; Champaign County, Illinois^{A}).

Notropis atrocaudalis.—Greene, 1927: 305 (Wisconsin^{A}). Wiebe, 1928: 161 (Minnesota River at Fort Snelling and St. Croix River above bridge^{A} [but not the record for Minnesota River above Cedar Avenue Bridge, which proves on re-examination of material to have been based on *N. h. heterolepis*]). O'Donnell, 1935: 482 (streams of Champaign County, Illinois^{A}).

Notropis heterolepis atrocaudalis.—Hubbs and Ortenburger, 1929: 67 (may be a distinct species^{A,P}; evidence of intergradation with *N. h. heterolepis* [false]; records from Arkansas River system in Arkansas and Oklahoma^{P}; characters^{P}; pale in silty water^{P}; Old River near Greenway, Arkansas, with reference to Meek^{I}).

Hybopsis atrocaudalis.—Jordan, 1929: 79 (range, Minnesota^{A} to Texas^{P}).

Notropis heterolepis (misidentification).—Thompson and Hunt, 1930: 98 (revised identification of *N. cayuga* from Champaign County, Illinois, also identified as *N. c. atrocaudalis*^{A}).

Notropis amnis amnis (accredited to Hubbs and Greene, but in no previous paper indicated as new).—Greene, 1935: 96–97, Map 37 ("pale, delicate minnow"^{A}; records and postglacial redispersal in Wisconsin^{A}; Mississippi River and large tributaries in Minnesota, Iowa, Wisconsin, Illinois, and Missouri^{A}; Ohio Valley to Great Pigeon River, Indiana^{I}; represented in Arkansas^{I,P}, Oklahoma^{P}, and Texas^{P} by a related subspecies). Eddy and Surber, 1943: 143 (southern Minnesota and Wisconsin southward to Missouri^{A}, Illinois^{A}, and Indiana^{I}; Mississippi River records from Greene^{A}). Gerking, 1945: 62 (Iroquois River, Indiana^{A}; White Creek, Lick Creek, and Big Pigeon River, Indiana^{I}).

Notropis amnis.—Lamb, 1941: 44 (5 collections, San Jacinto River system, Texas^{P}). Shoup, Peyton, and Gentry, 1941: 69 (3 records, Cumberland River system, Tennessee^{I}). Eddy and Surber, 1947: 162 (range, "southern Minnesota^A and Wisconsin^A southward to Texas^P''; Mississippi River records after Greene, 1935^A). Baughman, 1950: 130 (Texas^P).

The synonymy applies to the species as a whole. The matter that is applicable to *N. a. amnis,* to *N. a. pinnosa,* and to intergrades is indicated by the superscripts A, P, and I, respectively.

Diagnosis.—This is a small species of *Notropis,* not known to exceed 55 mm. in standard length. The mouth appears to be very small, for the upper lip reaches only to below the posterior nostril or very slightly beyond, though the upper jaw is really of average length: very distinctively, the posterior third of the upper jaw is nearly fleshless and is completely concealed beneath the suborbital; the width of the frenum of the lower lip equals the distance from the front of the gape to a line joining the corners of the gape. The pharyngeal teeth number 1, 4—4, 1; those in the main row are strongly hooked, smooth-edged, and provided with a flat grinding surface; those in the lesser row are weakly developed and are occasionally lacking on one or even both sides. Typically, there are 8 anal rays. The scales are rather large (34 to 37 in the lateral line) and are not especially elevated. The body is not markedly elevated or compressed and the eye is not less than one-fourth the length of the head. The upper surface is stippled, but not markedly darkened near the nape, along the base of the dorsal fin, or before the caudal fin; the predorsal stripe is weakly developed; on the entire upper sides dark edges line the scale pockets, but the head and body are devoid of melanophores below the lateral band, except on areas just behind the anus, along the base of the anal fin, and in 3 irregular files on the lower edge of the caudal peduncle; a dark stripe extends on the side of the snout, behind the eye, immediately above the lateral line on the trunk (with intensifications just above and just below each lateral-line pore), and along the lateral line on the urosome; it is expanded somewhat and truncated just in advance of the small, posteriorly frayed basicaudal spot; just above the dark band the dark pigment on the head and body fades out slightly to form a somewhat lighter streak (because the species commonly occurs in silty water, the dark pattern is often very faint, scarcely evident in life). The subhorizontal lips and the chin are wholly unpigmented. (Diagnosis by Hubbs and Greene.)

Comparisons and relationships.—In combination, the characters just stated serve to distinguish the species readily from all others. Its immediate relationships within the genus are not apparent, and it may be made the type of a distinct subgenus when *Notropis* receives the much needed general revision.

There appears to be no immediate consanguinity with *N. heterolepis* Eigenmann and Eigenmann ("*N. cayuga*" of authors), *N. atrocaudalis* Evermann, *N. volucella* (Cope), and *N. deliciosa* (Girard), the species with which *N. amnis* has usually been confused, because of superficial similarities. From these 4 species *N. amnis* differs in typically having a tooth in the lesser row, as well as in the peculiar mouth structure described above. From each of the other species it differs further in several ways: from *N. atrocaudalis* and *N. deliciosa,* in usually having 8 instead of 7 principal anal rays; from *N. heterolepis,* in having the dark lateral band less disrupted into black crescents; and from *N. volucella,* in not having the lateral-line scales especially elevated.

The minnow that *Notropis amnis* perhaps most closely resembles in superficial appearance is *Hybopsis amblops* (Rafinesque). The resemblance, in fact, is extremely close between the respective southern subspecies, *H. a. winchelli* Girard and *N. a. pinnosa,* the ranges of which are separated by the flood area of the lower Mississippi Valley (*H. a. winchelli* ranges westward to Amite River, 15 miles east of Baton Rouge, Louisiana, where specimens were collected by Nelson Marshall on December 30, 1939). Were it not for the very peculiar mouth structure of *N. amnis,* which *H. amblops* hardly shares, one might even postulate that *amnis* was derived from *amblops* by the loss of the small maxillary barbel. That possibility is not wholly excluded, for *H. a. winchelli* occasionally lacks the barbel on one or even both sides and the mouth structure somewhat approaches that of *N. amnis.* The concealed part of the maxillary remains shorter, however, and the width of the frenum of the lower jaw is only two-thirds the distance from the front of the gape to a line joining the corners of the gape.

Nuptial tubercles.—The isolated position of this species is emphasized by the strength and by the pattern of the nuptial tubercles. In the material at hand, these are well developed only in certain specimens of the southwestern subspecies from Texas, but the pattern was observed in examples from other localities and it is extremely improbable that the subspecies differ in tuberculation. The organs are particularly strong on the cheek, which they stud like a war club, standing, with swollen bases in contact, in 6 to 8 rows. A few large ones are scattered on the branchiostegals. Similar organs cover much of the preorbital region below the nostrils (leaving some lacunae), down to the rostral fold, with a few on the front of the maxillary. They become obsolete on the top and front of the snout, in advance of the nostrils. They line the orbit and cover the anterior interorbital region. They are sparse over the parietal region, but thick and strong in a band along the occipital line. They are well developed behind the eye and a few arm the upper part of the opercle. The occipital band extends onto the body scales and, in a narrow triangle thence backward to the origin of the dorsal fin, some of the scales bear a submarginal file of small bluntish tubercles. The anterior (or outer) two-thirds or three-fourths of the pectoral rays, except near their bases and tips, are thickened and armed on the upper surface with erect, pointed nuptial organs, grading outward from 1 series to 2 and then to a band, with many organs to each ray segment. The other fins are unarmed, as is the entire body except in the predorsal region. The specimen illustrated as Plate I, Figure 4, is a nuptial male, but the tubercles are not very obvious in the figure.

Range, habitat, and abundance.—*Notropis amnis* is one of many species confined to the Gulf drainage basin. It occupies the lowlands, from the larger rivers of the Mississippi River system in Minnesota, southward to the Gulf streams of Texas (Map 1). Toward the west it scarcely penetrates the tributary streams in Minnesota and Iowa and in the extensive fish survey of Missouri (by George V. Harry) it has been taken only in the Salt and Bourbeuse river systems and in the ditches and creeks of the depressed St. Francis Basin, all near the

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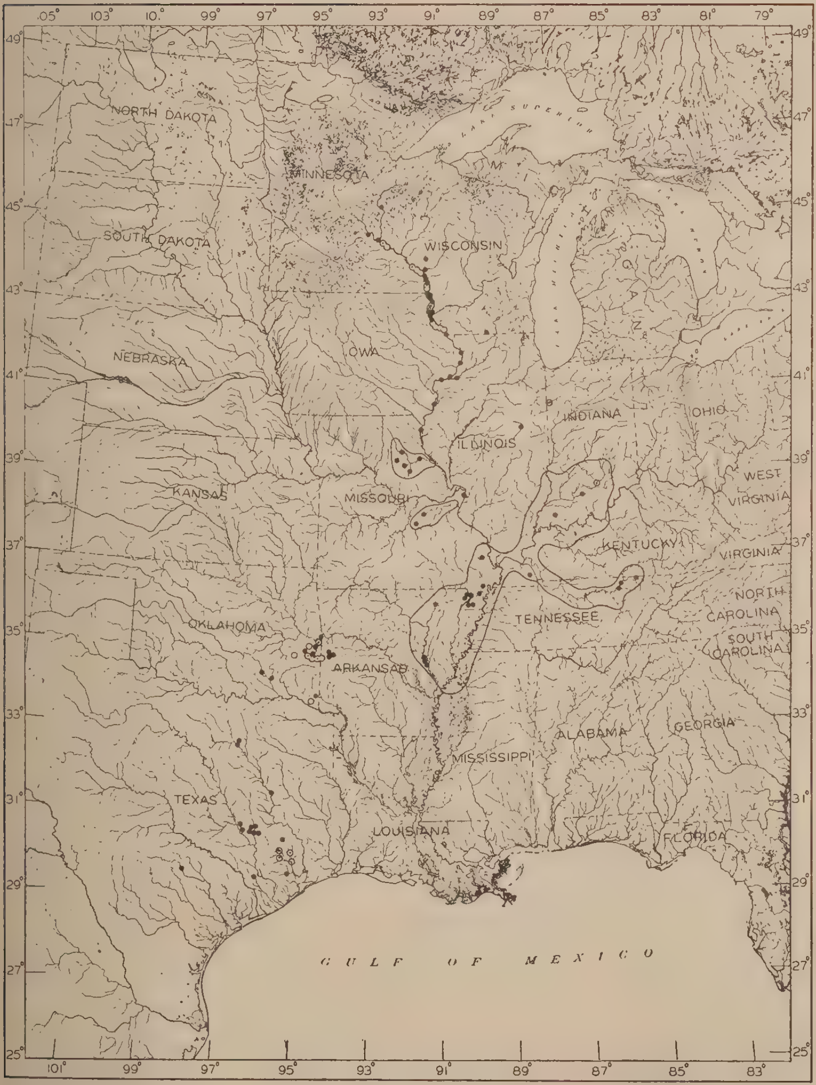
Map 1. Records and distribution of *Notropis amnis*, including subspecies *N. a. amnis* (northern) and *N. a. pinnosa* (southwestern) and intergrades, with the areas of intergradation outlined.

The hollow dots represent records unconfirmed by re-examination of the specimens. Those for the upper Mississippi River, stemming from the Upper Mississippi River Survey, were furnished by Raymond E. Johnson and John T. Greenbank and to large extent represent identifications by John D. Black; those from Indiana were published by Shelby D. Gerking; the ones from Oklahoma were provided by George A. Moore; those from Texas were published by Leonard D. Lamb.


NORTH DAKOTA
SOUTH DAKOTA
NEBRASKA
KANSAS
OKLAHOMA
TEXAS
MINNESOTA
IOWA
MISSOURI
ARKANSAS
LOUISIANA
WISCONSIN
ILLINOIS
INDIANA
OHIO
WEST VIRGINIA
KENTUCKY
VIRGINIA
TENNESSEE
NORTH CAROLINA
SOUTH CAROLINA
MISSISSIPPI
ALABAMA
GEORGIA
FLORIDA
LAKE SUPERIOR
LAKE MICHIGAN
LAKE HURON
GULF OF MEXICO
105° 103° 101° 99° 97° 95° 93° 91° 89° 87° 85° 83° 81° 79°
49° 47° 45° 43° 41° 39° 37° 35° 33° 31° 29° 27° 25°
101° 99° 97° 95° 93° 91° 89° 87° 85° 83°

Mississippi River. It lives in the White River system in Arkansas and in the Poteau River drainage basin and in adjacent waters of the Arkansas River system in Arkansas and Oklahoma. In the Red River system there are 4 records, all in southeastern Oklahoma. It is common in the streams of eastern Texas and penetrates westward in the Trinity River as far as Dallas. Toward the east it occurs, rarely, in a few Mississippi River tributaries in western Wisconsin, across Illinois, and barely into northern Indiana. It penetrates the Ohio River system, in great scarcity, to southwestern Indiana, to Kentucky near the mouth of the Tennessee River, and up the Cumberland River in Tennessee to near the Kentucky line. Below the Ohio River it has not been taken east of the Mississippi. Thus, the range extends to the west of the Mississippi in the south and almost entirely to the east of the Mississippi in the north. In consequence, the entire range is a band trending northeast from eastern Texas. Several other species have a similar distributional pattern. One, records of which have been plotted (Hubbs and Black, 1947: 29–33, Map 1), is *Ceratichthys vigilax.* Recent work shows that *C. perspicuus* is conspecific with *C. vigilax,* as formerly suspected, and warrants the deletion of the northwesternmost records for *C. v. perspicuus,* namely those in the Missouri River drainage basin of Iowa, Nebraska, and South Dakota, and those in northeastern South Dakota.

Toward the north, as its specific name implies, *N. amnis* is mainly confined to the larger lowland rivers; in the south, it more commonly inhabits small to medium-sized streams. Avoidance of the excessive turbidity of the main streams in the south may be the chief factor in this differential habitat selection, but temperature is perhaps also involved, for in the north this essentially southwestern species avoids the smaller streams, which are generally cooler, and may find only the larger waters sufficiently warm. The differential distribution corresponds rather well with the subspecies pattern (Map 1), as it does to some extent also in *Ceratichthys vigilax,* for *N. a. amnis* is primarily a large-river form, whereas *N. a. pinnosa* is more at home in smaller rivers and creeks. In the area of intergradation both large and small streams seem to be inhabited, though in Missouri the Mississippi River proper seems to be largely if not entirely avoided (the one record, for St. Louis, is based on a specimen collected more than 75 years ago by Louis Agassiz).

The relative abundance and general occurrence of the pallid shiner in the upper Mississippi River, in northern Illinois, Iowa, Wisconsin, and Minnesota, and its apparent scarcity or absence in the river farther south, no doubt reflect in part the more thorough collecting in the north, but may also be attributed to the excessive turbidity of the Mississippi below the mouth of the Missouri. As Reeve M. Bailey pointed out (in conversation), and as I also have noticed, a number of species become very scarce below the Missouri River, where their place is taken by such silt-loving forms as *Scaphirhynchus album, Hybopsis (Macrhybopsis) meeki, H. (M.) gelida, Hybopsis (Platygobio) gracilis communis,* and *Hybognathus placita.*

Within its area of abundance in the upper Mississippi River there seems to be a definite hiatus in the range of *N. a. amnis* (Map 1). The stretch of river for which there are no records for this shiner has been markedly altered by the inflow of the Chippewa River. In the northern half of the hiatus the Mississippi River is broadly and deeply ponded behind the barrier produced by the Chippewa Delta. For about a like distance downstream, as I am informed by John T. Greenbank, the main river conditions are modified by the vast quantities of sand brought in by the Chippewa. The lack of distributional records does not reflect inadequate collecting, for this section, as well as those above and below, has been thoroughly covered by the Upper Mississippi River Conservation Committee.

Although it seems to avoid excessive silt, *N. amnis,* according to the 40 records of ecological conditions accompanying the series in the University of Michigan Museum of Zoology, is tolerant of a wide range of turbidity, as well as of other environmental factors. The turbidity reports are about equally divided between "clear" or "almost clear" and moderately turbid or "muddy," with a few noted as "murky" or "very muddy." Aquatic vegetation was noted as absent about as often as present and was occasionally recorded as very dense. The records for the type of bottom vary from very soft mud, through sand and gravel to rock, with various admixtures of materials of different particle size. Summer temperatures grade from "cold" (presumably meaning cool) to "warm," with 2 records of nearly 23° C. for *N. a. amnis,* 6 readings averaging 29° for intergrades, and 5 more averaging 33° for *N. a. pinnosa.* The reports on current are about equally divided between "none" or "almost none" and "slow" to "rapid," with slow flows predominating over swift. The delicate fins and skin and the only moderately streamlined build conform with these habitat indications.

Except locally, *N. amnis* appears to be a very rare species, perhaps headed toward extirpation. In Minnesota and Wisconsin it has been proved by thorough collecting to be excessively rare except in the Mississippi River, its main tributaries, and immediately adjacent waters, and even in these waters it is estimated by Reeve M. Bailey and by John T. Greenbank to constitute less than 1 per cent of the minnow population. There are no records for Iowa away from the main river and the species apparently has been taken only twice in the interior of Illinois and only 4 times in Indiana, although much collecting has been done in these states. Only 1 specimen has come from Kentucky and only 3 small series from Tennessee. South of Iowa, except for the specimen taken by Louis Agassiz at St. Louis, Missouri, there are no records from the Mississippi or from east of that river. The very thorough collecting across Missouri has disclosed it to be moderately common only in the Salt River system and in the St. Francis Basin and elsewhere has yielded only 2 single-specimen samples from the Bourbeuse River of the Meramec River system (all tributaries to the Mississippi in the eastern part of the state). The Arkansas survey by John D. Black and earlier collecting in that state yielded only 2 samples from the St. Francis Basin, 4 from the White River system, and 3 from the Arkansas River system near the Oklahoma line. In Oklahoma the species has been taken once in the Arkansas River and only 4 times in the Red River system, in addition to samples from the Poteau River system, where it seems to survive in numbers. In eastern Texas the species is rather generally distributed and is locally common.

The scarcity of *Notropis amnis* is indicated by comparing its relatively few record stations (Map 1) with the multitudinous records for *Ceratichthys vigilax* (including *perspicuus*), a species with a similar distribution pattern and like ecological preferences.

NOMENCLATORIAL HISTORY.—Although it is rare over most of its range, *N. amnis* has been collected repeatedly since 1884 and has been reported under a number of names. It is surprising, therefore, that neither the northern or the southern subspecies yet bears a valid name. The fluctuating nomenclature is outlined and epitomized in the preceding synonymy, but requires some further elaboration and clarification.

The first specimens of *Notropis amnis* to be named and recorded were collected by Jordan and Gilbert in 1884 in Comal River at New Braunfels, Texas, and were included in a composite series to which they assigned the manuscript name *Notropis nocomis*. This name was entered, as a strict *nomen nudum,* in Jordan's list of North American fresh-water fishes (1885: 812). Jordan and Gilbert (1886: 23–24) then promptly abandoned the recognition of the series as a new species, but specified as the basis of *N. nocomis* their own specimens from the Comal, which they briefly described under the identification of *N. deliciosus.* Examination of their cotypes (U.S.N.M. No. 36531) has disclosed a complex comprising 55 specimens of *N. volucella* (recatalogued as No. 36531, lectoholotype, and No. 93516, lectoparatypes, of *N. v. nocomis*), only 7 of *N. amnis pinnosa* (paratypes No. 93514), and 2 "sleepers" each of *N. l. lutrensis* and *N. amabilis.* The specimens from San Marcos River at San Marcos, Texas (U.S.N.M. Nos. 36514 and 46219), which Jordan and Gilbert (1886: 22) also referred to *N. deliciosus* (with the statement that they do not differ evidently from specimens from the Des Moines River), were also catalogued as *N. nocomis.* They are reidentified *in toto* as *N. volucella nocomis* and are regarded as cotypes thereof (*N. a. pinnosa,* however, has recently been found in the San Marcos River). Those from Lampasas River at Belton, Texas (U.S.N.M. No. 36558), similarly reported by Jordan and Gilbert (1886: 19) as *N. deliciosus*, but catalogued originally as *N. nocomis,* are also referred to *N. volucella nocomis.* Jordan and Gilbert's description of the Comal River specimens definitely applies to the examples of *N. volucella,* which greatly predominated among their cotypes. Jordan (1891: 18) not long after recognized that Jordan and Gilbert had confounded 2 species. He qualified the one now identified as *N. amnis pinnosa* as "closely resembling *N. cayuga,*" which it does, superficially.

It seems that the name *Notropis nocomis* Jordan and Gilbert is nomenclatorially available in accordance with established rules and practices, since the description is recognizable in connection with the locality and general identification (see Opinion 52, International Commission on Zoological Nomenclature) and since it has generally been interpreted that the availability of a published name is not dependent on its acceptance by the original author. On the basis of this interpretation, the name *nocomis* is available for the southwestern creek subspecies of *N. volucella* that is represented by Jordan and Gilbert's specimens from the Comal, San Marcos, and Lampasas rivers in Texas. *N. v. nocomis* seems to range from the type locality (Comal River) and other streams in southeastern Texas northward to Missouri. It is one of several southwestern creek subspecies of *N. volucella,* none of which has been adequately defined in print. The status of the species and its northern subspecies has been treated by Hubbs and Raney (1947: 2–3), with references to previously published treatments.

The acceptance of the name *nocomis* as available under the date of 1886 and its application to a subspecies of *N. volucella* preclude its use for any other species. For this reason, *Notropis nocomis* Evermann (1892: 78–79) is regarded as an unavailable homonym. Under this name Evermann described and figured, as a "sp. nov.," another kind of *Notropis* that he regarded as indistinguishable from the species with which the same name was earlier associated by Jordan and Gilbert. Evermann's description and figure clearly apply to the form herein called *N. amnis pinnosa.* On re-examination, all cotypes from Trinity River at Magnolia Point, Texas, have been found to represent this species and subspecies. One of these cotypes, retaining the original catalogue number of the series (U.S.N.M. No. 45556), has been designated as the lectoholotype of *N. nocomis* Evermann (*nec* Jordan and Gilbert) and as the holotype of *N. amnis pinnosa* Hubbs and Bonham; the others (U.S.N.M. No. 93517) have been recatalogued as paratypes of the 2 nominal forms. The cotypes from San Marcos River at San Marcos, Texas (U.S.N.M. No. 58792) turned out to be *Dionda episcopa couchi* Girard, of which I collected 5 other specimens at the same locality on June 22, 1938. These misidentified cotypes were obviously not involved in Evermann's type description. The specimens referred to *N. nocomis* by Evermann, but not designated as types, have been reidentified as follows: the 1 from Buffalo Bayou at Houston, Texas (U.S.N.M. No. 69335) becomes a paratype of *N. amnis pinnosa;* of the 2 from Trinity River at Dallas, Texas, which Jordan and Gilbert collected in 1884, 1 is designated as *N. amnis pinnosa*

(U.S.N.M. No. 36475) and the other is an unidentified species of *Notropis.*

Soon after these complexities had been perpetrated, Jordan (1891: 17–18) initiated the confusion of *N. amnis* with "*N. cayuga*" by his qualification of Texas specimens (*N. a. pinnosa*) as "closely resembling *N. cayuga.*" Others followed this error, with the further confounding of *N. atrocaudalis* and "*N. cayuga*" (= *N. heterolepis*). Variously, these authors have reported *N. amnis* as *N. cayuga, N. cayuga atrocaudalis, N. heterolepis atrocaudalis, N. atrocaudalis,* and *N. heterolepis* (see synonymy). Currently, these 3 names are disposed as follows. *N. cayuga* Meek is a synonym of *N. bifrenata* (Cope), though most of the reports of *N. cayuga* were based on *N. heterolepis* Eigenmann and Eigenmann (Hubbs, 1926: 36, 40–41). *N. atrocaudalis* is obviously a full, valid species, confined so far as known to Texas, and differing from the northern *N. heterolepis* in having 7 instead of 8 anal rays, smaller hardly crescentic marks about the lateral line pores, bolder basicaudal spot, less conspicuous light band between the dark back and the lateral band, weaker margining of the scale pockets on the back, more oblique mouth, and in other respects. It differs further in habitat, for, according to Kirby H. Walker (personal communication), it occurs chiefly in the shallow, sandy, flowing sections of streams, rather than in the quiet weedy situations frequented by *heterolepis.* From other shiners with 4—4 teeth and 7 anal rays, *N. atrocaudalis* differs in numerous respects (Hubbs and Raney, 1947: 4–10).

Hubbs and Ortenburger (1929: 67) first suggested that a distinct species might be represented by the Mississippi River Basin minnow which had been confused with *cayuga, atrocaudalis,* and *heterolepis.* Along with all subsequent workers, however, they failed to appreciate that the same species had been described by Evermann as *N. nocomis.* On the basis of material collected on the Wisconsin fish survey, Hubbs and Greene confirmed the distinctiveness of this fish and, in manuscript, named it *N. amnis amnis.* This designation was used by Greene (1935: 96–97), but the brief characterization "pale, delicate minnow" does not satisfy the requirements of Article 25, Item *c* of the International Rules of Zoological Nomenclature.

The new species takes as its type description the following account of the typical subspecies, *N. a. amnis.* The southern subspecies, to which the name *N. nocomis* was invalidly applied, is also described as new, under the designation *N. a. pinnosa* Hubbs and Bonham. The intergrades are separately treated.

ETYMOLOGY.—The name *amnis* (used as the genitive of *amnis,* river) refers to the habitat of the type subspecies; *pinnosa* is from *pinna,* fin, and the suffix *-osus,* signifying the quality of abundance. The feminine termination is used because it is obvious, from the wording of the original description, that the final term of the generic name *Notropis* was derived from τρόπις (feminine), keel. Similarly, I use the feminine termination for species of *Hybopsis,* since ὄψις is feminine, and the neuter ending for species of *Scaphirhynchus,* since ῤύνχος is neuter. There is no valid reason for perpetuating the misinterpretation by zoologists of the gender of Greek words.

NORTHERN PALLID SHINER

Notropis amnis amnis Hubbs and Greene

(Pl. I, Figs. 1–2; Map 1)

TYPE MATERIAL.—We (Hubbs and Greene) retain as the types of *Notropis amnis amnis,* and hence of the species as well, the material from the Mississippi River and adjacent waters in Wisconsin, Iowa, and Minnesota that we utilized in diagnosing the species and subspecies prior to the first use of the name. The holotype (U.M.M.Z. No. 75435), an adult 43 mm. in standard length, was seined by Leonard P. Schultz and Clarence M. Tarzwell on August 27, 1928, in a channel of the Mississippi River, 1 mile north of Prairie du Chien, Crawford County, Wisconsin. There are 71 paratypes from this collection, 25 to 45 mm. long (U.M.M.Z. No. 78246, 3 now in the Museum of Comparative Zoology, No. 36079).

Other paratypes, with U.M.M.Z. catalogue numbers—and, in parentheses, the number of specimens—bear the following data:

Minnesota.—No. 72004 (2), Minnesota River at Fort Snelling, A. H. Wiebe, August 17, 1926.

Wisconsin.—No. 72022 (1), St. Croix River above bridge at Prescott, A. H. Wiebe, August 19, 1926; No. 76634 (3), Wisconsin River at Blue River Bridge, Grant County, C. Willard Greene and Laurence

C. Stuart, August 4, 1927; No. 76797 (2), Mississippi River at Cassville, Grant County, Greene and Stuart, August 10, 1927; No. 77705 (8), slough of Black River 5 miles east of Galesville, border of La Crosse and Trempealeau counties, like all following Wisconsin series collected by Leonard P. Schultz and Clarence M. Tarzwell in August, 1928; No. 77959 (1), St. Croix River above Never's Dam, 10 miles above St. Croix Falls, Polk County; No. 78186 (30), slough of Mississippi River 2 miles north of Victory, Vernon County; No. 78222 (18; 2 now in United States National Museum, No. 117559), slough of Mississippi River 3 miles south of Lynxville, Crawford County; No. 78279 (11), Mississippi River at Glenhaven, Grant County; No. 78312 (11), Mississippi River 0.5 mile above Wisconsin Bridge, near Dubuque (Iowa), Grant County; No. 78361 (8), Sugar River 6 miles east of Juda, Green and Rock counties.

Iowa.—No. 100918 (2), mouth of side slough of Mississippi River about midway between Lansing and mouth of Upper Iowa River, Carl L. Hubbs, August 5, 1932; No. 100949 (4), Mississippi River, 2 miles below Lansing, Hubbs, August 5, 1932.

All available record stations for nontype material, as well as the type and paratype localities just listed, are plotted on Map 1.

Range, habitat, and abundance.—The typical subspecies of *Notropis amnis* occupies the northern part of the range of the species, where it is mainly confined to the Mississippi River and adjacent sloughs and stream mouths (as is outlined on pp. 8–9). In these waters it appears to be of rather general occurrence, though it is seldom very abundant. There are very few records for the medium-sized to small streams of Wisconsin, Illinois, and Indiana and none for such waters in Minnesota or Iowa (Map 1).

The status of the subspecies across Illinois and in northern Indiana and the pertinence of the literature records call for some consideration. Three specimens from Rock River, northwestern Illinois, collected at Oxbow Island on July 10, 1925, seem to be *N. a. amnis*, though they were once desiccated (pectoral ray counts, 13—13 in 2, 13—14 in 1). Specimens typical of *N. a. amnis* came from Sugar River, southern Wisconsin, in the Rock River system. An adult specimen from the Sangamon River, 2 miles west of Dewey, Illinois, collected August 17, 1928, presumably the single example from Champaign County reported by Thompson and Hunt (1930: 24, 43, 98) variously as *Notropis cayuga, N. cayuga atrocaudalis,* and *N. heterolepis,* is particularly significant, for it came from deep within the state yet is fully typical of *N. a. amnis* in form, proportions, and pectoral ray count (12—13). It may therefore be assumed that other series from tributaries of the Illinois River, including Gerking's (1945: 62) from Iroquois River, Indiana, are referable to the typical subspecies.

Much doubt pertains to other published records from Illinois, particularly because of the confusion of *N. amnis* with the unnamed southern subspecies of *Notropis "cayuga"* (= *heterolepis*) having a complete lateral line. Under the heading *Notropis cayuga atrocaudalis* Forbes and Richardson (1909 and 2d ed., 1920: 134) reported: "ten collections of this minnow, containing thirteen specimens from the Illinois and adjacent waters, near Meredosia, and one from the main river at Havana. A specimen from Mackinaw creek in Woodford County, one from Anderson's branch, in Union county, and one from Little Fox River at Phillipstown may be referred with some uncertainty to this variety. Specimens taken at Greenway, Arkansas, by Dr. Meek, are, without much question, identical with the form here described." The Arkansas specimens are *Notropis amnis,* but I think that most if not all the Illinois records pertain to the southern subspecies of *N. heterolepis.* It is clear from the record of the number of collections of typical *cayuga* and from the assigned localities, that Forbes and Richardson included on their map for *N. cayuga* their 5 localities for *N. cayuga atrocaudalis,* misplacing the dot for the "Little Fox River at Phillipstown." An examination of all the "*Notropis cayuga*" specimens extant in the collection of the Illinois Natural History Survey discloses that the remaining collections of the 5 attributed to *N. c. atrocaudalis,* namely series from Meredosia and 1 specimen from Kappa (on Mackinaw River, on the border of Woodford County), represent the southern form of *N. heterolepis,* as do also collections that represent mapped records of "*N. cayuga*" from Pecunsagen Creek north of Utica, Sugar Creek at Milford, and Sangamon River at Mahomet. Unless contrary evidence is forthcoming, none of the specimens treated by Forbes and Richardson as *N. cayuga atrocaudalis* can be referred to *N. amnis* and the entire account, including the description, may be referred to the southern subspecies of *Notropis heterolepis.* I find no basis for O'Donnell's (1935: 482) statement that "*Hybopsis atrocaudalis*" is "found in small numbers in the Kaskaskia" and no evidence, other than the single specimen from Sangamon River mentioned above, that *N. amnis* occurs in "the streams of Champaign county."

In a broad band south of Iowa, Illinois, and northern Indiana all series examined appear to be intergrades (pp. 26–27), with the exception of a single specimen collected long ago at St. Louis, Missouri, by Louis Agassiz. This specimen, a mature female, was found in a series of *Hybognathus nuchalis* at the Museum of Comparative Zoology (M.C.Z. No. 1904) and was the basis for the inclusion of St. Louis in the range of "*Hybopsis nocomis*" by Jordan (1929: 78). It appears, from the notes I made in 1928, to be typical of *N. a. amnis,* as would be expected. It is a mature female with the body deeper (depth 4.0 in standard length), the back more elevated, and the snout sharper than in *N. a. pinnosa;* the dorsal fin begins over the pelvic insertion, nearer the caudal base than the tip of the snout; dorsal rays, 8; anal rays 8; teeth 1, 4—4, 1.

The available records indicate that this subspecies, like the intergrades and *N. a. pinnosa,* occupies a wide variety of ecological conditions, as is outlined for the species on pages 9–10. It probably occurs most frequently in moderately turbid water, with or without vegetation, on mud or sand bottom—for such conditions prevail along the main river.

SOUTHWESTERN PALLID SHINER

Notropis amnis pinnosa Hubbs and Bonham, new subspecies

(Pl. I, Figs. 3–5; Map 1)

Type material.—We (Hubbs and Bonham) designate as the holotype of *N. a. pinnosa* a specimen 45 mm. in standard length, U.S.N.M. No. 45556, discussed on page 11, along with paratypes first reported by Jordan and Gilbert and by Evermann. Other paratypes, all from Texas, are deposited in the University of Michigan Museum of Zoology and in the collections of the Agricultural and Mechanical College of Texas and the University of Texas. They came from localities represented by black dots on Map 1.

RANGE, HABITAT, AND ABUNDANCE.—*N. a. pinnosa* seems to be restricted to eastern Texas, where it is often rather common in small to medium-sized streams; to the tributaries of the Red River in eastern Oklahoma, where it is rare; and to the Arkansas River system in the region of the Poteau River in Arkansas and Oklahoma (Map 1). These records suggest that the range of *pinnosa,* like that of the intergrades, may be disrupted into several areas, or at least into regions of marked differences in abundance. Because of their high silt loads, the lower Red and Arkansas rivers, like the Mississippi below the confluence with the Missouri (p. 9), may serve as a distributional barrier. Since the St. Francis Basin and the lower and middle parts of the White River basin are occupied by intergrades, it is possible that the Arkansas River population of *N. a. pinnosa* is separated from the main part of the range of the subspecies, much as the Red River population of *Ceratichthys v. vigilax* is broken off by the southward extension of the range of the northern subspecies (*perspicuus*) in the lower waters. We should not, however, overlook the fact that very little field work has been done on the fishes of the lower parts of the Arkansas, Red, and Mississippi rivers, or on those of the streams between the Mississippi and the Trinity rivers; that is, in the region from which there are no records of *N. amnis.*

The account of the habitat of the species (pp. 9–10) was largely compiled from field records for this subspecies.

NOMENCLATURE.—The complicated nomenclature of this subspecies is reviewed in the analytical synonymy, with pertinent matter indicated by the superscript P, and is discussed on pages 10–14.

DIAGNOSIS AND SUBSPECIES COMPARISON.—*Notropis amnis pinnosa* checks with the specific diagnosis (p. 4) in all items and agrees more or less well with *N. a. amnis* in other characters. Points of agreement as well as discrepancy, both significant, are brought out in the following comparison and in the tables of counts and measurements.

After the subspecies had been separated on the basis of appearance and measurements, it was discovered that a moderately sharp separation could be made on the basis of the number of pectoral rays (with practice, these rays may be counted with precision under a binocular dissecting microscope, by using good illumination with moderately high magnification). The pectoral rays number 10 to 13 in 84 per cent of the specimens of *N. a. amnis* counted; 14 to 16 in 77 per cent of the *N. a. pinnosa* counts (Tables I and II). Thus, the 75 per cent separability now conventionally adopted for subspecies recognition is exceeded on this one criterion. The differentiation is sharper than

TABLE I

Fin Ray Counts in Subspecies and Intergrades of Notropis amnis

Principal rays are counted in the dorsal, anal, and caudal fins; all rays, including smallest rudiments, in the paired fins. In the dorsal and anal fins the last 2 elements are enumerated as 1 ray. Paired fins were counted and separately tabulated for both sides.

	Dorsal Rays				
	7	8	9	N	M ± SE
N. a. amnis	..	157	2	159	8.01 ± .01
Intergrades	3	108	3	114	8.00 ± .02
N. a. pinnosa	1	108	2	111	8.01 ± .02

	Anal Rays				
	7	8	9	N	M ± SE
N. a. amnis	3	151	4	158	8.01 ± .02
Intergrades	16	95	3	114	7.89 ± .04
N. a. pinnosa	12	118	1	131	7.92 ± .03

	Caudal Rays								
	15	16	17	18	19	20	21	N	M ± SE
N. a. amnis	..	..	1	4	94	8	2	109	19.05 ± .04
Intergrades	..	..	..	2	104	2	..	108	19.00 ± .02
N. a. pinnosa	1	..	1	4	95	..	..	101	18.90 ± .05

	Pelvic Rays							
	4	5	6	7	8	9	N	M ± SE
N. a. amnis	..	..	..	16	231	13	260	7.99 ± .02
Intergrades	1	..	..	11	209	7	228	7.96 ± .03
N. a. pinnosa	..	..	..	1	188	10	199	8.05 ± .02

	Pectoral Rays								
	10	11	12	13	14	15	16	N	M ± SE
N. a. amnis	2	12	67	168	45	3	1	298	12.86 ± .05
Intergrades	..	..	8	117	93	9	..	227	13.45 ± .04
N. a. pinnosa	..	1	5	42	146	15	..	209	13.81 ± .04

TABLE II

Percentage of Specimens Separable (or Identifiable) on Basis of Pectoral Ray Counts

Data from Table I.

	Pectoral Rays	
	10–13	14–16
Notropis amnis amnis	84	16
Intergrades	55	45
Notropis amnis pinnosa	23	77

TABLE III

Regional Variation in the Number of Pectoral Rays in Notropis amnis

	Number of Pectoral Rays								
	10	11	12	13	14	15	16	N	M±SE
N. a. amnis									
Upper Mississippi	2	12	67	168	45	3	1	298	12.86±.05
Intergrades									
Southern Indiana	..	..	..	3	1	2	..	6	13.8?
Cumberland River	..	..	..	17	9	..	..	26	13.35±.09
Kentucky	..	..	..	...	..	2	..	2	15.0?
Missouri									
Salt R. system	..	..	7	61	38	..	..	106	13.29±.06
Bourbeuse R.	..	..	..	1	3	..	..	4	13.75?
St. Francis Basin	..	..	1	22	32	5	..	60	13.68±.08
White R. system, Ark.	..	..	..	13	10	..	..	23	13.43±.10
N. a. pinnosa									
Poteau R. system	..	..	..	13	52	2	..	67	13.84±.05
Red R. system, Okla.	..	..	..	2	15	3	..	20	14.05±.11
Texas	..	1	5	27	79	10	..	122	13.75±.06

the figures indicate, for in *N. a. amnis* most of the fins with 14 rays had the lowermost ray extremely small, or were matched on the opposite side of the fish with a 13-rayed fin, whereas in *N. a. pinnosa* most of the 13-rayed fins had the lowest ray larger than usual, or were matched on the other side by a 14-rayed fin.

A main distinction, involving some overlap, is the relative shortening of the anterior parts and the elongation of the posterior regions in *N. a. pinnosa*. The differences show up in the figures (Plate I) and in the ranges and means for the appropriate measurements (Table IV),

TABLE IV

MEASUREMENTS AND SCALE COUNTS OF NOTROPIS AMNIS

The methods used are those proposed by Hubbs and Lagler (1941 or 1947). The measurements are expressed in thousandths of the standard length. The specimens of *N. a. amnis* are from the Mississippi River in Wisconsin and Iowa; 1 intergrade came from Wolf River, Tennessee; the 2 to 4 others, from the White River system, Arkansas; the *pinnosa* specimens are, respectively, from the Poteau River system in Arkansas and Oklahoma and from eastern Texas. The measurements and counts were made by Kelshaw Bonham, collaborating with the author.

Measurement or Count	Subspecies	Number	Minimum	Maximum	Mean
Standard length, mm.	*N. a. amnis*	14	30	44	38.8
	Intergrades	5	40	47	43.8
	Poteau (*pinnosa*)	5	43	47	44.8
	Texas (*pinnosa*)	23	34	55	44.1
Predorsal length	*N. a. amnis*	14	489	515	504
	Intergrades	5	487	511	498
	Poteau (*pinnosa*)	5	487	502	495
	Texas (*pinnosa*)	23	472	503	489
Prepelvic length	*N. a. amnis*	5	493	514	504
	Intergrades	3	491	499	496
	Poteau (*pinnosa*)	5	472	501	485
	Texas (*pinnosa*)	12	467	515	488
Body depth	*N. a. amnis*	5	200	240	221
	Intergrades	3	203	229	217
	Poteau (*pinnosa*)	5	195	227	214
	Texas (*pinnosa*)	12	199	280	234
Body width	*N. a. amnis*	5	132	141	137
	Intergrades	3	132	136	134
	Poteau (*pinnosa*)	5	129	138	134
	Texas (*pinnosa*)	12	125	163	146
Caudal peduncle depth	*N. a. amnis*	5	105	112	108
	Intergrades	3	106	114	109
	Poteau (*pinnosa*)	5	92	115	102
	Texas (*pinnosa*)	12	92	121	107
Caudal peduncle length	*N. a. amnis*	5	217	232	225
	Intergrades	3	210	240	223
	Poteau (*pinnosa*)	5	219	252	237
	Texas (*pinnosa*)	12	225	245	234.5
Head length	*N. a. amnis*	5	262	283	274
	Intergrades	3	273	280	277
	Poteau (*pinnosa*)	5	254	265	260
	Texas (*pinnosa*)	12	257	279	264
Head depth	*N. a. amnis*	5	165	172	168
	Intergrades	3	165	169	167
	Poteau (*pinnosa*)	5	155	163	159
	Texas (*pinnosa*)	12	152	184	167

TABLE IV (*Cont.*)

Measurement or Count	Subspecies	Number	Minimum	Maximum	Mean
Snout length	*N. a. amnis*	5	77	86	82
	Intergrades	3	81	86	83
	Poteau (*pinnosa*)	5	79	89	85
	Texas (*pinnosa*)	12	82	93	87
Eye length	*N. a. amnis*	14	78	87	83
	Intergrades	5	81	91	84
	Poteau (*pinnosa*)	5	71	75	73
	Texas (*pinnosa*)	23	66	81	74
Interorbital width	*N. a. amnis*	5	78	93	86
	Intergrades	3	83	87	86
	Poteau (*pinnosa*)	5	80	109	91
	Texas (*pinnosa*)	12	82	94	87
Upper jaw length	*N. a. amnis*	13	65	74	70
	Intergrades	5	61	78	68
	Poteau (*pinnosa*)	5	67	73	70
	Texas (*pinnosa*)	23	63	74	68
Gape width (between corners)	*N. a. amnis*	4	53	61	58.5
	Intergrades	3	58	61	59
	Poteau (*pinnosa*)	5	51	64	58
	Texas (*pinnosa*)	12	53	71	61
Dorsal origin to lateral line	*N. a. amnis*	5	112	143	131
	Intergrades	3	119	137	125
	Poteau (*pinnosa*)	4	119	123	121
	Texas (*pinnosa*)	12	118	151	136
Pelvic insertion to lateral line	*N. a. amnis*	5	97	103	100
	Intergrades	3	87	108	95
	Poteau (*pinnosa*)	4	96	102	100
	Texas (*pinnosa*)	12	91	136	111
Dorsal height	*N. a. amnis*	14	260	307	276
	Intergrades	5	265	280	273
	Poteau (*pinnosa*)	5	244	277	261
	Texas (*pinnosa*)	23	231	299	269
Anal height	*N. a. amnis*	5	208	218	213
	Intergrades	3	209	222	215
	Poteau (*pinnosa*)	5	190	217	205
	Texas (*pinnosa*)	12	180	238	211
Anal base	*N. a. amnis*	5	95	116	106
	Intergrades	3	104	111	107
	Poteau (*pinnosa*)	5	98	115	104
	Texas (*pinnosa*)	12	93	115	104
Caudal, longest ray	*N. a. amnis*	5	283	315	301
	Intergrades	3	303	316	308
	Poteau (*pinnosa*)	5	263	320	293
	Texas (*pinnosa*)	12	255	333	292

TABLE IV (*Cont.*)

Measurement or Count	Subspecies	Number	Minimum	Maximum	Mean
Pectoral length	*N. a. amnis*	5	203	215	209
	Intergrades	3	200	211	205
	Poteau (*pinnosa*)	5	168	212	195
	Texas (*pinnosa*)	12	177	221	193
Pelvic length	*N. a. amnis*	5	182	194	188
	Intergrades	3	185	200	190
	Poteau (*pinnosa*)	5	174	194	184
	Texas (*pinnosa*)	12	162	207	183
Scales above lateral line	*N. a. amnis*	5	4	5	4.8
	Intergrades	3	5	5	5.0
	Poteau (*pinnosa*)	5	5	5	5.0
	Texas (*pinnosa*)	12	5	5	5.0
Scales along lateral line	*N. a. amnis*	5	35	36	35.2
	Intergrades	3	34	36	35.3
	Poteau (*pinnosa*)	5	35	37	35.6
	Texas (*pinnosa*)	12	34	36	35.1
Scales below lateral line	*N. a. amnis*	5	3	4	3.8
	Intergrades	3	4	4	4.0
	Poteau (*pinnosa*)	5	3	4	3.8
	Texas (*pinnosa*)	12	4	5	4.25
Scales, pelvic to lateral line	*N. a. amnis*	5	3	4	3.6
	Intergrades	2	4	4	4.0
	Poteau (*pinnosa*)	5	3	4	3.8
	Texas (*pinnosa*)	12	3	5	3.75
Predorsal scales, midline	*N. a. amnis*	5	13	16	14.6
	Intergrades	2	13	19	16.0
	Poteau (*pinnosa*)	5	18	22	19.6
	Texas (*pinnosa*)	12	14	19	15.8
Predorsal scale rows	*N. a. amnis*	5	12	14	13.2
	Intergrades	2	11	14	12.5
	Poteau (*pinnosa*)	5	13	14	13.4
	Texas (*pinnosa*)	12	13	14	13.25
Scales around greatest depth	*N. a. amnis*	5	22	26	24.0
	Intergrades	3	24	26	24.7
	Poteau (*pinnosa*)	5	23	26	24.4
	Texas (*pinnosa*)	12	23	26	25.2
Scales around caudal peduncle	*N. a. amnis*	5	12	12	12.0
	Intergrades	3	12	12	12.0
	Poteau (*pinnosa*)	5	12	12	12.0
	Texas (*pinnosa*)	12	12	13	12.2

though some overlap is perhaps due to age and sex differences that are not separately analyzed and to incomplete precision in measuring. We note for *N. a. pinnosa* lower values for the predorsal, prepelvic, and head lengths and compensatingly higher values for the length of the caudal peduncle. A simple determination of the difference is made by stepping forward the distance from the caudal base (point of bending) to the extreme dorsal origin. In *N. a. pinnosa* the measurement extends to a point about one length of the eye in advance of the tip of the snout, varying from half the eye diameter (rarely less than that amount) to about twice the eye length. In *N. a. amnis* the point of the dividers in this measurement usually lies about one-fourth the eye length in advance of the snout, but may lie at any point from slightly behind the snout tip to nearly an eye's diameter before the snout. A point about 0.6 eye length in advance of the snout separates the measurements of about 80 per cent of the specimens of each subspecies. To some extent this measurement of the dorsal fin position also reflects the subspecific difference in the size of the eye.

In *N. a. pinnosa* the eye is usually less enlarged than in *N. a. amnis.* There is only a moderate overlap in the proportional measurements (Table IV). When stepped into the head length, the corneal length usually measures 3.4 to 4.0 times in the head, rather than 3.1 to 3.6 times. Perhaps in compensation, the snout averages the longer in *N. a. pinnosa* (Table IV). Furthermore, the snout in the southern subspecies is usually more gibbous and the head, consequently, is less pointed and less conical. Because of the smaller eye and often a longer upper jaw (not reflected by the measurements in Table IV), the upper jaw is usually a little longer than the eye in *N. a. pinnosa,* but is much shorter in *N. a. amnis.* Stepped into the head length, the upper jaw measures 3.5 to 4.3 times in *N. a. pinnosa;* 3.8 to 4.6 times in *N. a. amnis.*

Another average difference not brought out in Table IV is the body depth. Some of the specimens of *N. a. pinnosa* measured for this table came from populations with the body relatively deep, often as deep as in *N. a. amnis,* but more typically the southern form is the slenderer. In adults the depth in *N. a. pinnosa* usually enters the standard length 4.3 to 5.0 times; in *N. a. amnis,* 4.1 to 4.7 times.

In general the pigmentation in *N. a. pinnosa* is moderately well developed, but in *N. a. amnis* it is much reduced and concealed. This distinction no doubt reflects in large part the turbidity of the water, but in small part may be inherent.

There are also differences in general body form (Pl. I). *N. a. pinnosa* is typically more terete, for the body retains greater width in the mid-sections and posteriorly, is flatter across the back, and is less elevated at the dorsal origin (in the deeper specimens of *pinnosa* the body is usually deep and pudgy throughout, not markedly compressed toward the dorsal and caudal fins, and the dorsal contour is not sharply elevated at the front of the dorsal).

There is also an average difference in size that may be genetic. Some adults of *N. a. pinnosa* reach 55 mm. in standard length and many exceed 45 mm., which is the maximum known size of *N. a. amnis*, except in 1 lake collection, containing fish as long as 50 mm. (Diagnosis by Hubbs and Bonham.)

VARIATION.—Within *N. a. pinnosa,* even after the elimination of the more *pinnosa*-like intergrades, there is considerable local variation. Some populations approach *N. a. amnis* in 1 or a few characters, such as the depth of the body, the size of the eye, or even the number of pectoral rays. Included in the subspecies are some pool-and-riffle creek ecotypes with the fins unusually short and rounded (as is indicated by the low minimum and the low average proportions given in Table IV); elsewhere, the fins are unusually large and pointed. There is likewise much variation in the intensity of pigmentation. The specimens shown in Figures 3 and 5 on Plate I show differences in this respect, though the lighter one is by no means as pale as some examples of the subspecies. These 2 specimens differ also in one pattern feature, for in the lighter one (Fig. 3) the black specks along the anterior lateral line pores are more conspicuous than the dark streak on the trunk, whereas in the darker one (Fig. 5), the reverse is true.

The Red River and Arkansas River populations have apparently even higher average numbers of pectoral rays than those from Texas. In the forward position of the dorsal fin 3 specimens from Bachman's Lake, Dallas, Texas, are definitely extreme. Despite such local variations, a consideration of all characters suffices to identify each adequate series.

INTERGRADES

Notropis amnis: amnis × pinnosa

Between the ranges of the northern and the southwestern subspecies (Map 1) there are a number of more or less completely isolated populations of *Notropis amnis,* which, because of their intermediate or mixed characters, are treated as subspecific intergrades. The intermediacy is particularly well indicated by the pectoral ray counts, the single significant meristic character (Tables I–III). In form and proportions they are variably intermediate.

As their more or less complete and wide isolation would lead us to expect, the intergrade populations are not uniform. Of the 3 available specimens from southwestern Indiana the 1 from the Great Pigeon River has 13 pectoral rays on one side, as in *N. a. amnis,* and 14 on the other, as in *N. a. pinnosa,* and is apparently intermediate in other characters, and the 2 from Lick Creek, 2 miles east of West Baden, Orange County, are typical of *N. a. amnis* in form and general appearance, but 1 has 15 pectoral rays on each side (a high count even for *N. a. pinnosa*) and the other has 13 rays in each fin, as is usual for *N. a. amnis.* The Cumberland River population approaches *N. a. amnis* in the pectoral ray count, but in form and proportions is rather nearer *N. a. pinnosa.* The single individual from Kentucky (collected by Clarence M. Tarzwell and Henry H. Howell on October 18, 1942, in East Fork of Clark River, near the mouth of Tennessee River) would certainly have been referred to *N. a. pinnosa* had it come from the southwest, and may in fact represent a local stock inseparable from that subspecies; on geographical grounds it is provisionally retained in the intergrades. The series from Salt River in northeastern Missouri is closer to *N. a. amnis* than to *N. a. pinnosa* in pectoral ray number and is just intermediate in the position of the dorsal fin: when measured forward the distance from the caudal base to the dorsal origin usually extends to a point in front of the snout tip about 0.5 to 0.6 the eye length. The 2 specimens from the Bourbeuse River and the collections from the St. Francis Basin, from central-eastern and southeastern Missouri, respectively, are closer to *N. a. pinnosa* in pectoral ray counts, but somewhat nearer *N. a. amnis* in the position of the dorsal fin: the point just discussed is usually about 0.3 to 0.5 the eye length in advance of the tip of the snout. The White River specimens, from northeastern Arkansas, seem to be approximately intermediate in both characters.

The intermediate characters of these series from areas intervening between their respective ranges demand subspecific rather than specific status for the 2 forms here referred to *Notropis amnis.*

SUMMARY

Notropis amnis, new species, has been named, but never validly proposed. An outstanding character is the concealment beneath the preorbital of the relatively long and nearly fleshless end of the maxillary. The nuptial tubercles are strong. The synonymy is complicated. The name *N. nocomis* Evermann was based on the same species, but is reregarded as a homonym of *N. volucella nocomis* Jordan and Gilbert. The immediate relationships of *N. amnis* are not apparent. It is not closely related to *N. volucella, N. deliciosa, N. heterolepis,* or *N. atrocaudalis,* the species with which it has been confused. These forms are compared. *N. atrocaudalis* is a distinct species, confined to Texas. *N. amnis* ranges from Minnesota to the Gulf, chiefly in the main rivers in the north and in smaller streams in the southwest. The range trends northeastward from Texas. Wide ecological tolerance is shown,

TABLE V

Summary of Main Subspecies Differences in Notropis amnis

The distinctions are more fully outlined in the text (pp. 18–25) and are detailed in Tables I to IV.

Characters	Subspecies	
	N. a. amnis	*N. a. pinnosa*
Pectoral rays, including rudiments, typically	13 or fewer	14 or more
Distance from caudal base to dorsal origin usually extends to a point before tip of snout	Less than 0.6 eye length	More than 0.6 eye length
Eye length in head, usually	3.1 to 3.6	3.4 to 4.0
Depth of body in standard length, in adults, usually	4.1 to 4.7	4.3 to 5.0
Pigmentation typically	Very pallid	Moderate
Maximum known size (standard length)	45 mm. (50 mm. in 1 lake)	55 mm.

but excessive turbidity seems to be a barrier. On the basis of characters outlined in Table V the species is divided into the nominate northern form and a southwestern subspecies, *N. a. pinnosa* (new), with intergrades in more or less isolated intervening areas. The distributional and speciational patterns are much like those of *Ceratichthys vigilax.*

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PLATE I

Notropis amnis, new species, with 2 new subspecies. Photographs by Kelshaw Bonham.

FIG. 1. *N. a. amnis:* holotype, 43 mm. in standard length, from Mississippi River, Crawford County, Wisconsin.

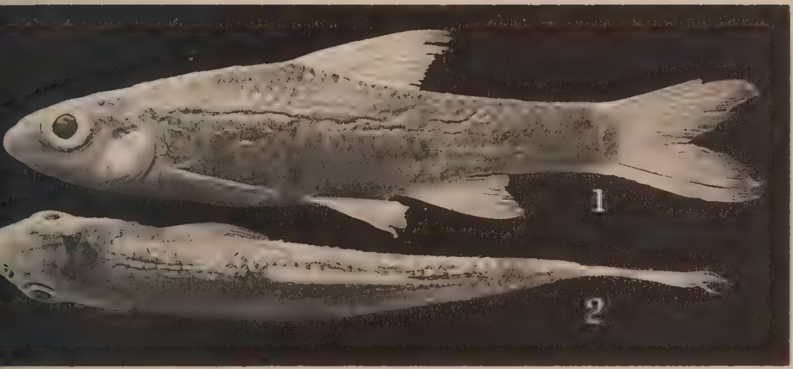
FIG. 2. *N. a. amnis:* dorsal view of adult paratype from slough of Mississippi River, Crawford County, Wisconsin (in series U.M.M.Z. No. 78222).

FIG. 3. *N. a. pinnosa:* adult paratype, 54 mm. long, from San Jacinto River, Harris County, Texas, collected by Kelshaw Bonham, Leonard D. Lamb, and party on October 13, 1940.

FIG. 4. *N. a. pinnosa:* dorsal view of mature male paratype from San Bernard River, between Austin and Wharton counties, Texas, collected by Kelshaw Bonham and A. Halloran on May 12, 1940.

FIG. 5. *N. a. pinnosa:* anterior half of adult paratype from Winter's Bayou, San Jacinto County, Texas, collected by Leonard D. Lamb on June 6, 1940.

PLATE I



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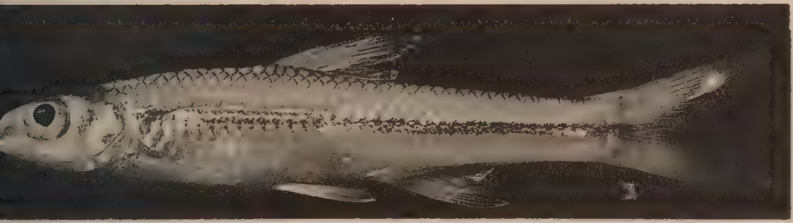

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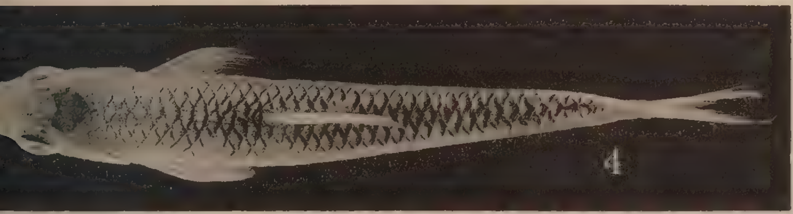

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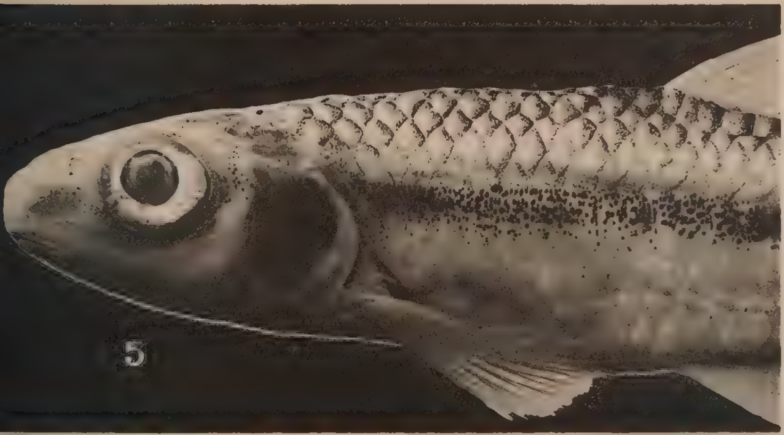

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Scripps Institution of Oceanography, Bull., Tech. ser., v. 6:1

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nerican Cyprinid Fish Notropis germanus Hay Interpreted as an Intergeneric Hybrid

CARL L. HUBBS

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Reprinted from

THE AMERICAN MIDLAND NATURALIST
Vol. 45 No. 2, pp. 446-454, March, 1951

The University Press
Notre Dame, Ind.

The American Cyprinid Fish Notropis germanus
Interpreted as an Intergeneric Hybrid[1]

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The systematization of our knowledge of the immense fresh-w
fauna of eastern North America is being advanced not only by the
of new forms and the reclassification of previously known species, bu
the elimination from the system of nominal species known only
original accounts. Some particularly troublesome forms are eliminated
being interpreted as interspecific hybrids, as was done when Raney
demonstrated that *Rhinichthys bowersi* Evermann and Goldsborough
on a hybrid between *Rhinichthys cataractae* (Valenciennes) and
micropogon (Cope). Such action, when taken on reliable grounds,
clarifies the systematics, but also contributes to the rapidly growing
facts and interpretations regarding hybridization in nature between fis
The present study clears the nominal species *Notropis germanus* Ha
252-253) from the system and adds a new interspecific hybrid, *Hyb*
hankinsoni × *Notropis heterolepis*. A somewhat similar combina
placita × *N. girardi*, has just been recorded by Cross (1950: 128,

A nomenclatorial complexity may arise from the circumstance
tropis germanus was proposed prior to the naming either of *Hyb*
hankinsoni Hubbs (in Jordan, 1929: 88) or of the still unnamed
subspecies of *Notropis heterolepis* Eigenmann and Eigenmann that
terized by the complete or nearly complete lateral line and that ma
volved in the hybrid combination. There is apparently no rule or reco
tion in regard to the availability of a name regularly proposed for a
species that is later interpreted as an interspecific hybrid. It might b
that the name was based on a complex and should be associated
element of the complex to be selected by the first author who recog
situation and unequivocally makes the selection. Such action has be
in respect to names based on subspecific intergrades and the distin
tween these and interspecific hybrids is often subjective and tenuous
1943). On the other hand, names based on interspecific hybrids ar
plicable to true populations and the type specimens would not be re
tive. More doubt, confusion and instability would arise from accept
from rejecting names interpreted as based on interspecific hybrids. It
fore recommended that these names be regarded as unavailable f
parental species. Such apparently has been the practice in both bo
zoology.

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[1] Contributions from the Scripps Institution of Oceanography, New Series,

HISTORY OF THE NOMINAL SPECIES

opis germanus was described by Hay (1887: 252-253), with stated
on, on the basis of a single specimen (U.S.N.M. No. 37949) that
ollected in Smoky Hill River, in the Missouri River system, at Wallace,
Colorado border in Kansas. Meek (1894: 136) misidentified the
reserved specimen with the very different northern species *Notropis*
n (Cope). This error was obviously the basis for the inclusion
as within the range of *N. heterodon* in all editions of Jordan's
of the Vertebrates from the 5th (1888: 55) to the 12th (1916: 55)
subsequent manuals, whether using the name *Notropis heterodon*
1923: 77) or that of *Hybopsis heterodon* (Pratt, 1935: 74; Schren-
1938: 135-136; Driver, 1942: 274). Jordan and Evermann (1896:
d Evermann and Cox (1896: 369, 402, 425) also included *N. ger-*
n the synonymy of *N. heterodon* and the error was repeated by
Evermann and Clark (1930: 136), under the name *Hybopsis het-*
By the elimination of Kansas from the stated range of *Hybopsis*
n (Jordan, 1929: 79) and of *Notropis heterodon* (Hubbs and
1941: 58; 1947: 66), *N. germanus* tacitly has been removed from
nymy of *N. heterodon*. This rectification leaves the range of *N.*
n compact and consistent.

clear from the original description that Hay was uncertain as to the
N. germanus. Since the type specimen, however, has some very
e characters, yet shows no signs of abnormality, and since he wrote
e critical and clarifying evaluation of natural hybrids, it was only
hat he should have named the form. He probably appreciated the
iacy of some of the generic characters, for he said that "were the in-
canal not so short—shorter than the body—the specimen might be
to *Hybognathus* (*Dionda*) *nubila* Forbes" (*Dionda nubila* is rather
iate between *Hybognathus* proper and *Notropis*, but has the intestine
ore convoluted than it is in the type of *N. germanus*). The pharyn-
h, as described, are generically intermediate, though they were not so
d. Overemphasizing a partial similarity to *N. deliciosa*, Hay com-
germanus only with that species.

IDENTIFICATION OF THE HYBRID

ief study of the type specimen of *Notropis germanus* in May, 1933,
d me that it was either an otherwise unrecognized species or, much
ely, a hybrid between *Hybognathus hankinsoni* and some species of
. Perhaps swayed by Hay's alignment of his species with *N. deliciosa*
ng that the specimen approached *deliciosa* more closely than any of the
ecies taken by Hay at the same locality, I provisionally interpreted it
rid between *Hybognathus hankinsoni* Hubbs and *Notropis deliciosa*
sis (Cope). This view was published by Breukelman (1940: 374).
and faded condition of the specimen hindered precise determination.

ore penetrating analysis of the characters, on April 7, 1950, convinced
the second parental species was not *N. deliciosa*, nor any other species

collected at the same locality, but almost certainly was *Notropis heter*
Before entering into a discussion of the species involved, however, we s
consider the presumed parental genera.

THE PARENTAL GENERA

The interpretation of an otherwise unidentifiable specimen as a h
hybrid between the long-intestined genus *Hybognathus* and the short-g
group *Notropis* needs occasion no great surprise or doubt. On the ba
such criteria as were used in the interpretation of many catostomid fish
terspecific hybrids (Hubbs, Hubbs and Johnson, 1943: 11-14), convi
grounds have already been found for identifying a considerable numb
cyprinid specimens as hybrids between *Hybognathus* and the closely r
genus (or subgenus) *Dionda* on the one hand and *Notropis* and other
intestined genera on the other hand. Among the dozens of interspecific
binations that have thus far been recognized among the Cyprinidae of e
North America, chiefly on the basis of unpublished researches at the U
sity of Michigan Museum of Zoology, are many that seem to involve pa
genera less closely related than are *Hybognathus* and *Notropis*. Thu
very aberrant genus *Campostoma* appears to hybridize occasionally with
diverse groups (genera and subgenera) as *Nocomis, Rhinichthys, Semo*
Clinostomus, Chrosomus, Luxilus (subgenus of *Notropis*), and *Dionda*
the modern view that fish groups with a long gut were repeatedly ev
from others with a short gut (Hubbs and Turner, 1939: 17; Hubbs, 1
188), *Hybognathus* (with *Dionda*) has been interpreted as a recent off
from *Notropis* or an allied genus (Hubbs and Brown, 1929: 29). The
idea, that the long-intestined and short-intestined minnows belong to two
tinct evolutionary lines, was already doubted by Jordan and Evermann (1
202-204) and has now been abandoned.

One parental species is identified as a *Hybognathus* and the other
Notropis primarily on the basis of the structure of the intestine, the phary
teeth, and the jaws.

The intestine describes 2 definite, not very tightly compacted S-sh
loops, one behind the other, as in no known species of cyprinid in ea
North America. In all the many and varied species of this region the inte
has either a single compressed S-loop or several to many coils. Only a h
could be expected to have such an intestine. Many characters exclude
consideration *Chrosomus, Pimephales* and *Campostoma,* the long-gutted g
other than *Hybognathus* to be expected in the region. On the basis of th
testinal convolution the other parental genus could have been any of the s
gutted genera of the area, but on the basis of other characters, that gen
inferred to have been *Notropis*. The apparently silvery peritoneum also
gests hybridization, for it is inconsistent with the somewhat elongated intes
A blackening of the peritoneum in the Cyprinidae almost invariably ac
panies a lengthening of the gut (Hubbs, 1941: 188).

The pharyngeal teeth correspond with the assumption that the par
species were a *Hybognathus* and a *Notropis,* each with a 4—4 tooth form
The number is given in the original description as 4—4, with the state

teeth have "a distinct masticatory surface" and that the first tooth is The left arch, which alone remains with the specimen, has characters nfirm the hybrid determination. The arch is thick and somewhat much as in *Hybognathus,* but the moderately broad slope below the the main row shows no trace of the attachment of small teeth. The of the main row have rather broad grinding surfaces, less well devel- an in *Hybognathus* but better formed than in *Notropis.* Instead of hooks, as in *Hybognathus,* or of being rather strongly hooked, as is n *Notropis,* the teeth in this regard are intermediate: the first and third rom above) are rather weakly hooked, whereas the second and fourth ks.

he structure of the jaws, which resemble those of *Dionda nubila, N. us* definitely appears to be a *Hybognathus* × *Notropis* hybrid. The w is too slender for a *Notropis* and, like that of *Dionda* or *Hybog-* has a symphyseal knob. The mouth is only slightly oblique and is of e size: the length of the upper jaw enters the head length 4.3 times. uth is smaller than would be expected in a hybrid between *Hybognathus* er *Nocomis* or *Semotilus,* and too large and too oblique for expectation *bognathus* × *Phenacobius* combination. Thus the short-gutted genera egion other than *Notropis* (Breukelman, 1940: 370-371) seem to be ed from consideration.

THE PARENTAL SPECIES

e doubt can be attached to the identification of the *Hybognathus* is *H. hankinsoni* Hubbs. As indicated by Breukelman (1940: 371) eidentified as *H. hankinsoni* the 2 specimens of this genus (U.S.N.M. 37) that Hay took with the type of *Notropis germanus* and reported 253) as *H. nuchalis.* In the only moderately elevated and rounded, ll falcate dorsal fin (depressed length 1.6 in distance to occiput and 2.6 nce to tip of snout) and in the vertically oval scales with numerous e type of *N. germanus* definitely resembles *H. hankinsoni* as con- with *H. nuchalis* (Hubbs and Lagler, 1941: 50; 1947: 58) or with *ita.*

inarily one finds both parental species of a natural hybrid among associated in the same collection, and among these *N. deliciosa* best ectations. *N. topeka* would fit almost as well, but none of the other ls listed by Hay from the same locality has characters that could plaus- inferred to combine with those of *H. hankinsoni* to produce a fish re- g the type of *N. germanus.* These additional species are *Semotilus ulatus atromaculatus* (Mitchill), *Nocomis biguttatus* (Cope), *Phena- nirabilis* (Girard), *Notropis cornuta frontalis* (Agassiz) ("*megalops*"), *tropis lutrensis lutrensis* (Baird and Girard). *N. lutrensis* was listed nce perhaps by error for another species.

fin-ray formula (D 8, A 9, C 10+9, P_1 13—13, P_2 8—8) is not ly significant except for the number of anal rays. The characteristic in the species most plausibly involved is 8 for *Hybognathus hankinsoni tropis heterolepis* and 7 for *Notropis deliciosa* and *N. topeka.* Since

in ray numbers hybrids are almost invariably intermediate between the pa
species, *N. deliciosa* and *N. topeka* are almost surely eliminated. Fu
more, the anal rays in the hybrid are fine and delicate, not approachi
strength and thickness the rays of *N. deliciosa* and *N. topeka*. It wou
plausible to assume that the parental species other than *H. hankinsoni*
or more anal rays, but the only species known from northwestern K
(Breukelman, 1940: 370) that normally have more than 8 anal rays, n
Notropis cornuta frontalis (Agassiz) and *N. lutrensis lutrensis* (Bair
Girard), both seem to be excluded from consideration by reason of their
bodies and numerous other characters that are not suggested by the h
in which the depth of the body is only one-fifth the standard length.
tional species with 9 or more anal rays that conceivably might have occ
in Smoky Hill River have other characters that would almost certainl
combine with those of *H. hankinsoni* to produce a fish like "*N. germa*
Since the hybridity of this "species" seems almost certain, we are forc
infer that the *Notropis* parent had 8 anal rays, as does *N. heterolepis*.
anal rays in the type are unusually fine and crowded, especially towar
posterior end of the fin, as they usually are in specimens of any species
have an abnormally high ray count.

The tooth formula (4—4) of the hybrid favors a like formula i
Notropis parental species, but would not certainly exclude one with a 1,
1 tooth formula. *N. heterolepis, N. deliciosa* and *N. topeka* all hav
formula 4—4.

The squamation is significant, though the standard formula as give
Hay (5—35 or 36—4) is not very critical (I counted 34 scales in the l
line series, but the scales are now largely destroyed). The number of
around the caudal peduncle seems much more meaningful. These nu
only 12, with 5 above and 5 below the lateral line. In *H. hankinsoni* a
N. deliciosa missuriensis and *N. topeka,* all from northwestern Kans
count 15 or 16 scales around the peduncle. It is certainly not to be exp
that 12 peduncular scales would ensue from the crossing of 2 species,
with 15 or 16 scales. *N. heterolepis* has 12 scales around the peduncle
thus again fits expectation much better than do the other species na

In its slender body (depth about 5.0 in standard length) and espe
in the slender, protracted form of the caudal peduncle, the hybrid als
sembles *N. heterolepis* much more than *N. deliciosa missuriensis* (a ch
subspecies) or *N. topeka* (a robust species). The least depth of the ped
enters the head length 2.7 times and the peduncle length 2.6 times.

The rather flat upper contour of the head and the slenderness of the
(depth 1.7 in length) further point toward *N. heterolepis* and away
N. deliciosa missuriensis and *N. topeka*. Other proportions, such as th
of the eye (corneal length 4.0 in head), the length of the upper jaw (4
head), the broad head, and the position of the dorsal fin (its origin more
a pupil's length nearer tip of snout than base of caudal), agree with
culated expectation for a hybrid between *Hybognathus hankinsoni* and *No*
heterolepis. A hybrid with either *N. d. missuriensis* or *N. topeka* w
probably have a smaller eye.

:oloration also the type of *N. germanus* is more suggestive of *N. hetero-* an of *N. d. missuriensis* or *N. topeka* (*Hybognathus hankinsoni* is iformly pigmented). The lack of pigment on the chin is particularly int and, of course, negates the identification of *N. germanus* with *N. on.* Hay described the color as quite dark above, with broad dusky on all the scales. Traces remain of this color, though the scale-pocket seem to have been weak in a light streak above the dark lateral band nostic feature of *N. heterolepis*). The distinct dusky streak running the silvery sides and the especially prominent dark streak on the nd on the opercle, as described by Hay, duplicate just what would be l in a *hankinsoni* × *heterolepis* hybrid. The black dots described as the lateral line pores suggest the coloration of *N. d. missuriensis* and *ka,* but the faded remnants of these "dots" suggest that these markings finitely larger and more prominent than in those species and approached centic dark marks on the lateral-line scales of *N. heterolepis.* There is agreement with or approach toward *N. heterolepis* in the prominence ge size of the melanophores on the top of the head, in the dark general on, and, especially, in the development of melanophores in the peritroct. gion in *N. heterolepis* as in *N. volucella* is punctulate, but in *N. delici-* liagnostically devoid of black pigment (Hubbs and Lagler, 1947: 61). sicaudal spot is not conspicuous.

ich subspecies of *Notropis heterolepis* was involved in the cross is indeterminate. The southern form scarcely differs from the nominal ies in any respect other than the complete or nearly complete lateral d few scales remain on the type of *N. germanus.* The very few in the ries show no distinct pore and it is thought possible that *N. h. hetero-* is the subspecies involved. That subspecies occurred in the headwaters South Platte River in Colorado (see below) and may have been the one ed in the Smoky Hill River near the Colorado border of Kansas.

ZOOGEOGRAPHICAL AND ECOLOGICAL CONSIDERATIONS

nay be objected that one putative parental species, *N. heterolepis,* has een reported from the Smoky Hill River or immediately adjacent and seems to be absent now throughout Kansas, but that situation has ays existed. This minnow is known to have occurred formerly south as north, and west as well as east of Smoky Hill River and it presumably abited that stream. The species seems to have become greatly depleted most areas extirpated throughout the southern part of its range. A e-examination of the specimens shows that Jordan (1891: 18), under ne of *N. cayuga,* reported the southern subspecies of *N. heterolepis* to mon in the Arkansas River at Wichita, in southern Kansas. No other or specimens from Kansas have been encountered by John Breukelman V. Ralph Taylor, in their studies of the fishes of this state. This sub- with some intergrades, was recorded as *N. cayuga* by Evermann and 1896: 401) from numerous localities in Nebraska and adjacent states. orough surveys of Nebraska from 1939 to 1941 by Raymond E. John-)octoral Dissertation, University of Michigan, 1942) disclosed no evi-

dence of its continued existence in that state, save in one restricted r
northern relicts in the Sand Hills. From Colorado (Juday, 1904: 11
227; Cockerell, 1908: 167, 169, 171; Ellis, 1914: 49) the species h
reported solely on the basis of specimens collected in 1903 in the Sout
system at Longmont. A specimen from Longmont in the National N
is referable to the typical subspecies. Repeated tries in 1950 by
C. Beckman and staff to collect further specimens in the same regi
failed. In Iowa, the species has become very scarce, if it survives at all
M. Bailey, personal communication; Harrison, 1949: 337). As el
indicated (Hubbs, 1951), Forbes and Richardson (1909: 134),
as *N. cayuga* and in part as *N. cayuga atrocaudalis,* reported the s
subspecies of *N. heterolepis* from several localities in central and s
Illinois, where the species is now extirpated or nearly so. This su
seems to remain common only in Missouri and even in that state is lo
scattered. In the Museum of Zoology of the University of Michigan
a single series of the same subspecies from Tennessee. In Indiana (
1945: 65, map 49) the species is extremely rare, except in the glacia
and in Ohio (Milton B. Trautman, personal communication) it
extirpated over most of its primeval range.

The widespread depletion and general extirpation of *Notropis het*
throughout the southern part of its range is attributable to the deterior
the habitat. This is one of the minnows that prefers cool, clear, weedy
(Hubbs and Lagler, 1941: 59-60; 1947: 68) and such primeval con
as a result of agricultural practices, have largely been eliminated south
limits of Wisconsin glaciation.

That *Notropis heterolepis* may well have lived in the Smoky Hil
prior to the excessive cultivation of the Plains is suggested by the occ
there in 1885 (Hay, 1887) of other species generally characteristic
clear waters, such as *Nocomis biguttatus* (probably now extirpated th
cording to Breukelman, 1940: 370), *Semotilus a. atromaculatus, N*
cornuta frontalis and *Hybognathus hankinsoni.*

It is inferred that *Notropis heterolepis* was on the road to extirpa
Smoky Hill River when Hay made his collections in 1885 and that th
nant was inclined to hybridize with other species. The tendency of a
ing species to hybridize with others was suggested by Greene (1935: 87
his discussion of *Clinostomus elongatus* in Wisconsin and Michigan.
eral, it seems to be true that the scarcity of a fresh-water fish species,
due to recent establishment or to impending extirpation, is especially co
to hybridization with other species (Hubbs and Brown, 1929: 28, 36;
Hubbs and Johnson, 1943: 39, 47-48, 63; Hubbs, Walker and Johnson,
4, 8-9, 15, 19-20; Hubbs and Hubbs, 1947: 151-154).

On distributional and ecological grounds it is plausible to assum
Hybognathus hankinsoni and *Notropis heterolepis* may hybridize. Bot
to prefer cool, weedy waters, chiefly in northern regions (Hubbs and
1941: 59-60; 1947: 68). These species often occur together and ma
have similar reproductive proclivities, in respect to season, habitat and be

SUMMARY AND CONCLUSIONS

en nominal species that have complicated the system are reliably inter- as interspecific hybrids a contribution is made not only to systematics o to natural genetics. Names based on such hybrids are regarded as able for either parental species. "*Notropis germanus*," from Kansas, is eted as a hybrid, *Hybognathus hankinsoni* × *Notropis heterolepis*. Ex- the number of anal rays (9), the characters of the type and only known n of *germanus* are consistent with this interpretation and the crowded ys suggest an abnormally high count. No other species that might ccurred in western Kansas, other than *N. heterolepis*, has characters uld be expected to combine with those of *H. hankinsoni*, which was one parental species, to produce such an offspring. As usual, most ers of the hybrid are intermediate.

view of the very extensive pattern of interspecific hybridization among an Cyprinidae, this determination occasions no great surprise, even the inferred parental species are very unlike structurally. The dif- s are largely associated with nutrition and have less taxonomic weight ey were formerly thought to have.

is assumed that *N. heterolepis* in the southern part of its range was on the now nearly completed road to extermination, as the result of ural practices, when Hay collected the hybrid in 1885. In line with bservations, it is presumed that the scarcity of this species was con- to its hybridization with other forms. This propensity may well accel- he extirpation of species that have become rare through a deterioration environment.

ACKNOWLEDGMENTS

e M. Bailey of the University of Michigan Museum of Zoology has offered very and constructive suggestions. Further criticism has come from Milton B. Trautman ranz Theodore Stone Laboratory. Leonard P. Schultz has provided specimens and m the United States National Museum. William C. Beckman has checked the extirpation of *Notropis heterolepis* in Colorado.

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NEW CYPRINID FISHES OF THE GENUS *NOTROPIS* FROM TEXAS *

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During the past three decades the known freshwater fish fauna of eastern North America, one of the richest in the world, has been further augmented by the discovery of many new species. Unfortunately, pressure of other duties has prevented the formal naming of a considerable proportion of these discoveries. The three new species of *Notropis* from Texas here treated—*oxyrhynchus, brazosensis* and *potteri*—are among the fishes for which the initial published descriptions have been unduly withheld. Since further delay would interfere with the researches and publications of other ichthyologists and fishery biologists, these species are now diagnosed.

The three species are apparently confined to eastern Texas, for they have never been collected in the extensive surveys of surrounding regions, namely northeastern Mexico (Hubbs and Gordon, MS), New Mexico (survey in progress by William J. Koster), Oklahoma (work begun by Ortenburger and Hubbs, 1926, and Hubbs and Ortenburger, 1929 *a-b*, and now being continued by George A. Moore), and Louisiana (more cursory collecting).

These shiners, especially *oxyrhynchus* and *brazosensis,* abound in the very silty water of the Brazos River and its main tributaries, which are thus shown to have a somewhat distinctive fauna. As native species, *N. oxyrhynchus* and *N. potteri* seem to be confined to the Brazos River system (the population of *N. potteri* currently existing in and about artificial Lake Texoma in the Red River system, between Texas and Oklahoma, is interpreted as the result of the establishment of escaped bait minnows). The range of *brazosensis* extends into adjacent coastwise waters.

The discovery of these new species in Texas occasioned no great surprise, for the varied fish fauna of this large state has been little studied and very seldom reported upon since the compilation by Evermann and Kendall (1894).

Following the recognition by the senior author of these species as new, counts and measurements were made by the junior author in 1940, in accordance with the specifications proposed by Hubbs and Lagler (1941: 12-20, figs. 2-3; 1947: 8-15, figs. 2-6). Angles were measured as recommended by Hubbs (1946). The calculations were also made by Bonham and the photographs were taken by him. The final draft was prepared in 1950 with the much appreciated cooperation of Dr. Reeve M. Bailey of the University of Michigan Museum of Zoology. Prof. Frank T. Knapp of the Agricultural and Mechanical College of Texas kindly dropped in our favor his plan to describe the three species, which he also has collected. He has contributed specimens and ideas helpful in determining the status and relationships of

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* Contributions from the Scripps Institution of Oceanography, New Series, No. 503.

N. potteri. Dr. George A. Moore of Oklahoma Agricultural and Mechanical College has provided critical material from the Red River and from within Oklahoma, and has contributed useful suggestions.

All specimens herein reported for the three new species are deposited in the University of Michigan Museum of Zoology and in the Agricultural and Mechanical College of Texas.

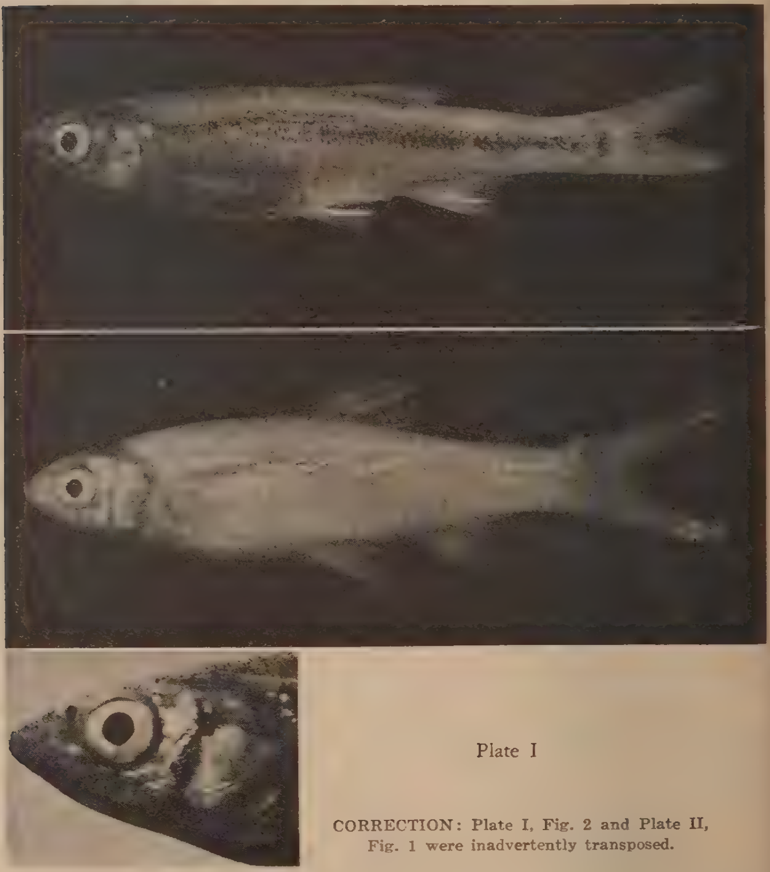

Plate I

CORRECTION: Plate I, Fig. 2 and Plate II, Fig. 1 were inadvertently transposed.

Fig. 1. *Notropis percobromus*: adult specimen (University of Michigan Museum of Zoology, No. 127636), collected in Arkansas River near Oxford, Kansas, by C. E. Burt, on June 15, 1939. All photographs were taken by Kelshaw Bonham.

Fig. 2. *Notropis oxyrhynchus*: topotypic paratype, an adult, 54 mm. in standard length, collected in Brazos River at Wellborn Crossing, Texas, by Kelshaw Bonham and class, on October 25, 1940.

Fig. 3. *Notropis oxyrhynchus*: head of the holotype, an adult 50.8 mm. long, collected in Brazos River at Wellborn Crossing, Texas, by Kelshaw Bonham and class, on October 21, 1938.

SHARPNOSE SHINER

Notropis oxyrhynchus, new species

Pl. I, Figs. 2-3

In both ecological and taxonomic view this striking species appears to be the southern representative of *N. percobromus* Cope (Pl. I, Fig. 1). Since that species has seldom been mentioned and has usually been confused with other forms, its history and status call for clarification. It was described, as *Alburnellus percobromus*, by Cope (1871: 440) from specimens collected at St. Joseph, Missouri, presumably in the Missouri River or some adjacent water (Jordan and Evermann gave the type locality definitely as the Missouri River at St. Joseph). Under the name *Minnilus percobromus* the species was accepted as valid by Jordan and Gilbert (1883: 202), but it was synonymized with *N. rubrifrons* (=*N. rubella*) by Jordan and Evermann (1896: 295). Accepting this synonymy, Fowler (1910: 290) based his description of *rubrifrons* in part on the types *A. percobromus*, one of which he figured (pl. 21, fig. 50). Swayed by these actions, Hubbs and Ortenburger (1929*b*: 83-85) wrongly resurrected Cope's name for the southwestern representatives, still unnamed, of *N. rubella*. They had the true *percobromus* as well, however, but treated it as "*Notropis*, species?" (1929*a*: 34; 1929*b*: 86). Only recently (Hubbs, 1945: 16-17) has the true distinctive status of *percobromus* been pointed out, along with the indication that it inhabits the silty waters of the Great Plains from the Missouri River system in the Dakotas to the Red River (of the South), with tongues extending down the main rivers into Arkansas and presumably into Missouri, even to the Mississippi River in Tennessee (Reeve M. Bailey, in personal communication, has indicated his belief that the records from the upper Mississippi River system were based on misidentified specimens of *N. a. atherinoides*). This statement of range is based on the identification by the senior author of many series in the Museum of Zoology of the University of Michigan.

Although it resembles *rubella* in certain respects, such as the anteriorly deep body, the sharp nose and the large mouth, *oxyrhynchus* seems to belong, with *percobromus*, to the *atherinoides* rather than to the *rubella* series of the subgenus *Notropis*, as these series were distinguished by Hubbs and Ortenburger (1929*b*: 83-84).

N. oxyrhynchus agrees rather well with *percobromus* and contrasts with *atherinoides atherinoides* in several of the characters by which those forms were distinguished in tabular form by Hubbs (1945: 17): the head is relatively large, more than one-fourth the standard length; the eye is submedian,

TABLE I

ANAL RAY COUNTS IN FIVE SPECIES OF *Notropis*

	Anal rays (frequencies)										
Species	6	7	8	9	10	11	12	13	No.	Av.	S.E.
N. percobromus	....	....	....	....	40	40	8	2	90	10.69	.08
N. oxyrhynchus	....	....	....	7	61	14	....	....	82	10.69	.06
N. brazosensis		4	94	8	....	....	....	....	106	8.04	.04
N. illecebrosa	....	....	12	31	4	1	....	....	48	8.87	.09
N. potteri	1	81	3	....	....	....	...	....	85	7.02	.02

dorsoventrally; and the lips are not conspicuously blackened anteriorly. In other characters *oxyrhynchus* resembles *a. atherinoides* more closely than *percobromus*: the predorsal scale pockets are generally, though not always, clearly marked by rather definite marginal files of melanophores, and the body is usually rather slender, though some examples are deeper than the more attenuate specimens of *percobromus*. In the slope of its mouth *oxyrhynchus* further resembles *atherinoides* more closely than *percobromus*, the mouth of which is more strongly oblique than it is in most related species: the angle seen in lateral view between the closed mouth and the long axis of the body ranges from 32° to 38° in *oxyrhynchus*, is about 35° in *atherinoides*, and is typically 48° or more in *percobromus*. The head is much slenderer than in *percobromus*, averaging even slenderer than in *a. atherinoides*: the head depth is usually contained about 1.7 times in the head length. The height of the dorsal fin is contained 1.5 to 1.9 times in the

TABLE II

MEASUREMENTS (IN THOUSANDTHS OF STANDARD LENGTH) AND COUNTS OF *Notropis oxyrhynchus* FROM TEXAS AND *N. percobromus* FROM KANSAS AND OKLAHOMA

Species	Notropis oxyrhynchus			N. percobromus	
Specimens	Holotype	24 Paratypes (Range)	Mean	10 Adults	
				Mean	Range
Standard length, mm.	50.8	28.4—48.9	40.5	37.7	36.9—49.6
Predorsal length	581	534—571	558	575	567—587
Dorsal to occiput	394	334—377	355	386	371—404
Prepelvic length	528	489—533	512	505	498—515
Body depth	252	194—263	228	255	227—291
Dorsal origin to lateral line	165	140—178	157	156	142—183
Pelvic insertion to lateral line	83	50—97	77	102	97—125
Body width	154	119—162	141	150	128—180
Caudal peduncle length	185	175—206	192	189	176—207
Caudal peduncle depth	114	100—121	111	102	94—108
Head length	264	246—306	276	270	260—281
Head depth	173	158—194	174	178	170—186
Snout length	83	77—93	86	77	72—80
Eye length	63	59—73	66	67	60—73
Fleshy interorbital	87	78—94	85	92	85—98
Upper jaw length	95	89—105	95	88	83—96
Mouth width [1]	59	48—67	56	58	47—64
Dorsal height	211	189—237	213	215	200—233
Anal height	163	158—187	168	178	163—201
Anal base	127	119—153	137	139	124—163
Pectoral length	205	178—235	205	207	189—227
Longest caudal ray	264	264—355	287	282	252—306
Pelvic length	152	129—153	144	157	143—168
Scales					
Above lateral line	7	6—7	6.84	6.70	6—7
Along lateral line	35	34—37	35.8	37.1	36—38
Below lateral line	4	3—4	3.68	3.90	3—4
Lateral line to pelvic	4	3—4	3.52	3.70	3—4
Predorsal scales	25	20—26	22.2[2]	21.3	19—24
Predorsal rows	20	16—21	18.5	18.4	17—20
Around body: Above	15	13—15	14.5[3]	14.0	13—15
Below	11	9—14	11.8[3]	11.0	10—12
Total	28	24—31	28.0	27.0	26—29
Around caudal peduncle: Above	8	7—9	7.71[3]	6.90	6—7
Below	6	5—7	5.76[3]	5.00	5—5
Total	16	14—18	15.7	13.9	13—14
Fin Rays					
Dorsal	8	8—8	8.00	8.00	8—8
Anal	10	9—11	10.1[4]	10.7[6]	10—13
Pectoral	14—15	13—15	13.9[5]	14.5[5]	13—16
Pelvic	8—8	7—8	7.96[5]	8.00[5]	7—9

[1] Between ends of gape.
[2] 7 specimens.
[1] 17 specimens.
[4] 82 specimens, see Table I.
[5] Both sides counted.
[6] 90 specimens, see Table I.

distance forward to the occiput (in this respect *oxyrhynchus* is intermediate). The measurements of *oxyrhynchus* and *percobromus* are compared in detail in Table II.

The outstandingly distinctive feature of *oxyrhynchus,* as contrasted with either *percobromus* or *atherinoides,* or, in fact, with almost any other species of the genus, is the form of the muzzle, which is very sharp in either dorsal or lateral view. The front angle of the top of the head is only 15° to 17°, as contrasted with 19° to 23° in *N. percobromus.* The angle formed by the dorsal and ventral contours of the muzzle, 56° to 70°, is usually much narrower than in *percobromus* (72° to 85°), particularly in the smaller fish. The angle of the head proper in lateral view is only 43° to 50°. The conical appearance of the head (Pl. I, Fig. 3) is enhanced by the continuous and almost straight, rather than distinctly angulated line formed by the margins of the interopercle and the mandibular ramus. The dorsal contour of the snout also tends to be straighter than in *percobromus,* and less decurved. The margins of the rami as seen from below are almost straight and converge forward evenly throughout their length, rather than generally being divergent forward to beyond the middle of the length of the rami. In further correlation with the more conical form of the head, the muzzle in *oxyrhynchus* is longer than in *percobromus*: in adults the snout is consistently much longer than the eye, on the average 29 rather than 15 percent longer, and the upper jaw is 1.2 to 1.6 times as long as the eye, instead of being only a little longer.

The anal rays average 10.09, slightly fewer than in *percobromus* (Table I). The scales in the lateral line average fewer, those around the caudal peduncle more numerous (Table II). The lateral line is more decurved, as is indicated by the lesser proportional distance between the lateral line and the insertion of the pelvic fin. *N. oxyrhynchus* seems to be a more silvery fish than *percobromus.* The distribution of melanophores is shown on Plate I, Figures 2-3.

The general form is rather distinctive. The ventral outline (Pl. I, Fig. 2) is more curved than the dorsal. Though it bisects the eye, a straight line from the anterior tip of the upper lip to the middle of the caudal base lies distinctly above the middle of the head. The dorsal contour rises in a gentle arch from the acuminate muzzle to the origin of the dorsal fin, which is well behind the middle of the body. From the vertical through the dorsal origin the upper and lower contours converge backward in slightly concave lines. Forward from the anal fin the slope continues downward to about the middle of the belly and then curves upward to the isthmus.

Fundamentally, *oxyrhynchus* agrees with the other members of the subgenus *Notropis.* The hooked teeth number 2, 4—4, 2. The slightly falcate anal fin typically has more than 9 rays (Table I). The dorsal fin begins well behind the insertion of the pelvic. The silvery color, slender form, strongly curved ventral contour, oblique mouth and sharp snout stamp it, like the other species of the subgenus, as a midwater to near-surface swimmer.

TYPES.—The holotype (University of Michigan Museum of Zoology, No. 129829), an adult 50.8 mm. in standard length, was seined from Brazos River at Wellborn Crossing, Brazos County, Texas, on October 21, 1938, by Kelshaw Bonham and party from the Agricultural and Mechanical College of Texas. Many paratypes were collected in Brazos River at four places: at the holotype locality, on October 21, 1938, and on October 25, 1940; at

Government Dam, near Navasota, on November 24, 1939, and December 3, 1939; west of College Station, on October 12, 1939; and at Kappes Bridge, southwest of College Station, on September 29, 1941. Smaller series were obtained in Navasota River, 16 miles southeast of College Station, on October 6, 1939; in Little Brazos River, at State Highway 21, on June 13 and July 13, 1940 (breeding adults included); and in the lower end of Toweash Creek, another tributary of the Brazos. The last-named series was collected by Marion Toole, the one from Kappes Bridge by G. H. Soulen, the others by Kelshaw Bonham and students.

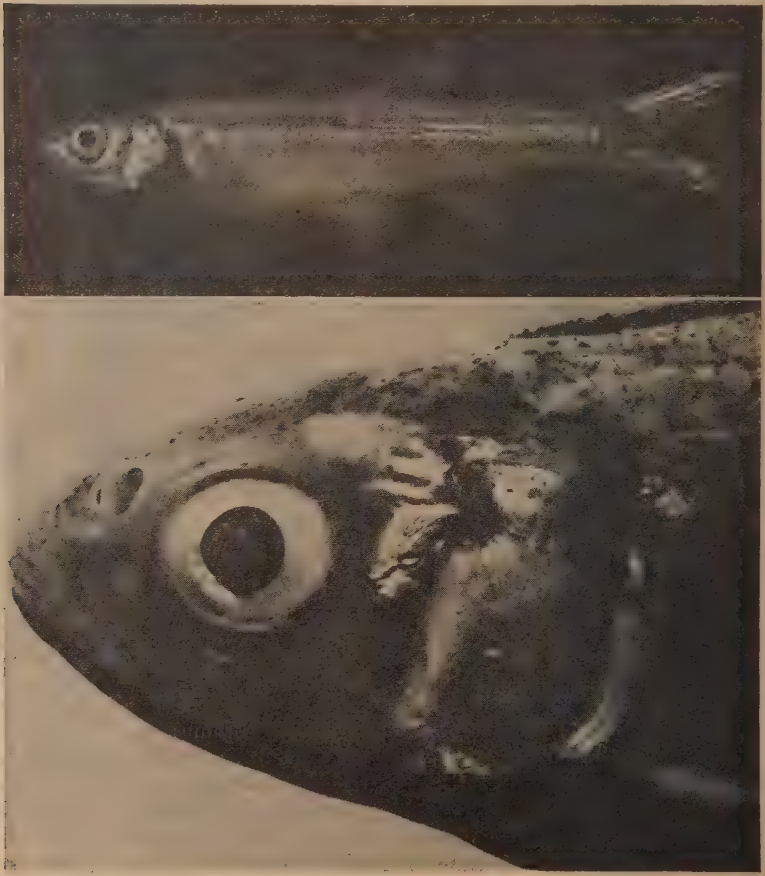

Plate II

Fig. 1. *Notropis brazosensis*: topotypic paratype, an adult 46 mm. long, collected by Kelshaw Bonham and class, on October 25, 1940.

Fig. 2. *Notropis brazosensis*: head of holotype, an adult 49.2 mm. long, collected in Brazos River at Wellborn Crossing, Texas, by Kelshaw Bonham and class, on October 21, 1938.

CORRECTION: Plate I, Fig. 2 and Plate II, Fig. 1 were inadvertently transposed.

The name *oxyrhynchus* is derived from Greek words transliterated into Latin as *oxys* (sharp) and *rhynchus* (snout). Though the gender of *Notropis* is feminine and though the species name is regarded as a compound adjective, it is given the *-us* ending because that is the Latin transliteration of the normal feminine ending for Greek compound adjectives.

BRAZOS SHINER
Notropis brazosensis, new species
Pl. II

In the maze of species that constitute the genus *Notropis*, in the broad sense to which we have adhered, this new one appears to be most closely related to *N. illecebrosa* (Girard). In fact, *N. brazosensis* seems to be the southwestern representaive of *illecebrosa,* which ranges through the silty waters of the large rivers in the Mississippi Valley from Illinois to Louisiana. The status of the true *illecebrosa,* which had been confused with other species, was clarified by Ortenburger and Hubbs (1926: 126) and by Hubbs and Ortenburger (1929*a*: 29).

From *illecebrosa* this species differs in usually having 8 instead of 9 anal rays (Table I). Jordan and Evermann (1896: 268) reported the anal rays as 8 in the types of *Alburnops illecebrosus* Girard, perhaps as a miscount or misprint, or perhaps because the count was made on a variant specimen or on one of the specimens of *N. boops* that were mixed in the same series.

The difference in number of anal rays would suffice for no more than subspecific separation, but other distinctions (Table III) warrant treatment of the forms in full species. Especially significant are the differences in the structure of the mouth, the pharyngeal arch, and the teeth.

The rays in the fins other than the anal are alike in number (Table IV). The number of pelvic rays is rather characteristic, for most species of *Notropis* have 8 pelvic rays.

OTHER CHARACTERS.—The body contours are symmetrically curved on either side of the horizontal line extending from the front of the rather strongly oblique mouth through the center of the eye to the middle of the caudal base. The muzzle is bluntly conical in side view. The lips are relatively thin and the upper lip is scarcely expanded at the midline.

The fins are moderately pointed and rather expansive. The dorsal and anal are distinctly falcate; the pectoral and pelvic, somewhat blunt at the tip. The dorsal origin is near or a little behind the middle of the standard length, about over or a little behind the pelvic insertion. The dorsal height often nearly equals the length of the head and occasionally exceeds that dimension. The caudal fin is usually longer than the head.

The complete lateral line is rather strongly downcurved anteriorly. Its scales are scarcely modified in outline. Scale counts are detailed in Table V.

The general color is pale and silvery, with rather sparse puncticulation above the midsides and virtually none below. Large melanophores are scattered deep beneath the broad and rather diffuse silvery band. The band broadens anteriorly and covers the side of the head behind the eye. Above this silvery band and along its upper part is a narrow dusky streak comprising small superficial melanophores. The dark streak is arched upward to nearly parallel the dorsal contour, but on the caudal peduncle it becomes submedian. Between the dorsal origin and the pelvic insertion this streak and the lateral line divide the body approximately into thirds. The dusky

TABLE III

COMPARISON OF *Notropis brazosensis* WITH *N. illecebrosa*

Based chiefly on a series of paratypes of N. **brazosensis** (U.M.M.Z., 159368, from Little Brazos River at Highway 21, Brazos County, Texas) and on a collection of N. **illecebrosa** (U.M.M.Z., 153072, from Mississippi River at Brasher or Cottonwood Point, Pemiscot County, Missouri).

Character	N. brazosensis	N. illecebrosa
Anal rays (Table I)	Typically 8	Typically 9
Fins	Usually less elevated and less pointed; pelvic not or barely reaching anus	Usually much elevated and pointed; pelvic reaching about to, or beyond, anus
Size and texture	Larger and coarser	Thinner, more delicate
Fin rays	Thicker and stronger	Thinner, more fragile
Upper lip	About even with snout tip; profile of tip about vertical or sloping downward and more or less backward; mostly visible from directly below	Usually projecting beyond snout tip; profile of tip sloping downward and more or less forward; little or not at all visible from directly below
Lower lip	Definitely included within upper lip	Approximately even with upper lip
Upper limb of pharyngeal arch	About one-half as broad (at base) as long; outer edge rather evenly curved; upper limb longer than lower	About two-fifths as broad (at base) as long; outer edge angulated; upper limb shorter than lower
Lower (anterior) edge of grinding surface of main pharyngeal teeth	Scarcely cultrate and jagged	More or less strongly cultrate and jagged
Row of melanophores along anal base and on lower edge of peduncle	Becoming obsolescent in half-grown	Remaining strong in half-grown; obsolescent in adult

TABLE IV

FIN RAY NUMBERS IN *Notropis brazosensis* AND *N. illecebrosa*

The anal ray counts are given in Table I. The counts for N. **illecebrosa** were all taken from the series noted in Table III.

	Dorsal Rays				
	7	8	9	N	M
N. brazosensis	1	85	1	87	8.00
N. illecebrosa	....	45	4	49	8.08

	Caudal Rays				
	18	19	20	N	M
N. brazosensis	3	70	1	74	18.97
N. illecebrosa	2	35	1	38	18.97

	Pectoral Rays					
	13	14	15	16	N	M
N. brazosensis	3	73	85	12	173	14.61
N. illecebrosa	2	33	31	4	75	14.58

	Pelvic Rays				
	8	9	10	N	M
N. brazosensis	54	117	3	174	8.71
N. illecebrosa	20	77	1	98	8.81

streak is separated by a narrow almost unpigmented light band from the dorsal area, where melanophores in single file line the scale pockets. Near the dorsal midline other melanophores lie inside the marginal file. There is a narrow dusky streak before, along and behind the dorsal base. Before the dorsal the more prominent melanophores are arranged in one series; behind the dorsal, in two or three series. There is a weak dusky triangle just before the dorsal base but none at the caudal base or at the nape. The basicaudal spot is barely suggested. Fine melanophores line the dorsal and caudal rays and occur on the outer edge of the pectoral. The top of the head is dark on the parietal region and is dusky between the eyes and between the nostrils. The melanophores extend over the snout onto the upper lip and occasionally onto the lower lip and the tip of the chin. Fine dots are sprinkled between the nostrils and the mouth and a narrow streak follows the lower margin of the orbit. Very few melanophores occur about the upper part of the opercles. Except as noted the lateral and ventral surfaces of the head are unpigmented.

Minute nuptial tubercles, sharp and recurved, follow the second to the ninth pectoral rays, in a single file branching once, with about 4 to 6 tubercles (or pairs) on each ray segment. Elsewhere the nuptial organs are almost completely obsolete.

Proportional measurements are analyzed in Table V.

TABLE V

MEASUREMENTS (IN THOUSANDTHS OF STANDARD LENGTH) AND SCALE COUNTS OF TYPES OF *Notropis brazosensis*

	Holotype	24 Paratypes (Range)	Mean
Standard length, mm.	49.2	33.5—61.5	44.1
Predorsal length	500	498—537	513
Prepelvic length	504	478—528	504
Body depth	252	217—289	243
Dorsal origin to lateral line	165	134—184	160
Pelvic insertion to lateral line	98	74—119	91
Body width	153	125—184	147
Caudal peduncle length	206	193—226	205
Caudal peduncle depth	128	108—124	116
Head length	250	249—282	262
Head depth	183	167—198	179
Snout length	72	71—87	77
Eye length	59	57—80	70
Fleshy interorbital	99	91—102	97
Upper jaw length	78	73—90	80
Mouth width [1]	63	51—69	58
Dorsal height	240	217—270	243
Anal height	172	158—204	178
Anal base	116	102—128	110
Longest caudal ray	272	256—313	288
Pectoral length	197	177—222	201
Pelvic length	161	144—184	168
Scales			
Above lateral line	6	5—7	6.04
Along lateral line	34	33—35	34.1
Below lateral line	4	3—4	3.76
Lateral line to pelvic	3	3—4	3.20
Predorsal scales	14	13—20	14.8
Predorsal rows	14	12—17	14.0
Around body: Above	13	12—14	12.6
Below	11	9—11	10.8
Total	26	23—27	24.8
Around caudal peduncle: Above	6	4—7	5.28
Below	5	4—6	5.00
Total	13	11—14	12.3

[1] Between ends of gape.

HABITAT AND RANGE.—Like *oxyrhynchus,* this species is characteristic of the silty waters of Brazos River and its main tributaries, in eastern Texas. The form of the body, the position of the mouth and eye, the color and other features suggest a mid-water habitat. It is often, perhaps usually, associated with *oxyrhynchus* and the two commonly dominate the fauna. Outside the Brazos system *brazosensis* is known to us only from adjacent waters near the coast, including San Bernard and Colorado rivers, to the southward, and, doubtfully, from one locality in Harris County, to the northward (see below). Recent collecting by Clark Hubbs in the Neches River system has failed to disclose this species there.

TYPES.—The holotype (University of Michigan Museum of Zoology, No. 129827), an adult 49.2 mm. in standard length, was seined with the type series of *oxyrhynchus* from Brazos River at Wellborn Crossing, Brazos County, Texas, on October 21, 1938, by Kelshaw Bonham and party from the Agricultural and Mechanical College of Texas. Several series of paratypes were collected at other points in the Brazos River system, by Bonham and others. The 24 paratypes measured for Table V were obtained at 5 places: at the holotype locality; in Brazos River west of College Station, on October 21, 1938; in Little Brazos River at State Highway 21, on June 13 and July 13, 1940 (including breeding adults); in borrow pit 5.3 miles west of Bryan on highway 21, on July 13, 1940; and in San Bernard River at State Highway 60, on May 12, 1939.

Additional paratypes of this species were collected by Bonham and party at 3 localities in Brazos County: in Brazos River west of College Station, on October 12, 1939; in Little Brazos River near Bryan, on March 31, 1939; and in Navasota River at Ferguson Crossing, on October 6, 1939. Still others were taken by R. T. Richey in Little Brazos River, Brazos County, on March 23, 1936, and by A. H. Wright in Colorado River, on the road between Houston and Victoria, on June 24, 1917.

A single large specimen collected by J. L. Baughman at Old River Terrace, on Market Street Road, Harris County, on May 18, 1941, is referred doubtfully to *brazosensis.* It agrees with that species in most respects, but has only 7 anal rays. More material is urgently needed from this region north of the mouth of Brazos River—not only of this species but also of the fish fauna in general.

CHUB SHINER

Notropis potteri, new species

Pl. III

Notropis potteri.—Potter, 1938: pl. 4, upper fig., facing p. 422 (probably a recognizable figure; species attributed on legend to Hubbs; no text reference; "recently located in McLellan County, Texas"). Baughman, 1950: 130 (name attributed to Hubbs; no description whatever; "common in Brazos River and tributaries"; entry taken from manuscript list by Bonham and Reid).

This species is described as new, despite the fact that Potter published, over the name *Notropis potteri* Hubbs, a figure that is probably recognizable, when the assigned locality is considered. Potter's action failed to satisfy the requirements for availability stipulated by Article 25, Item C of the International Rules of Zoological Nomenclature, however, because the date of publication was subsequent to 1930 and because neither a diagnosis nor a definite bibliographic citation was furnished.

DIAGNOSIS.—The hooked pharyngeal teeth number 2, 4—4, 2. Fin rays: dorsal, consistently 8; anal, usually 7, rarely 6 or 8 (Table I); pectoral, 14 to 18, averaging 15.7; pelvic, typically 8, rarely 9, averaging 8.07.

The fins are moderately large and rather bluntly pointed: the dorsal height is always less than the head length, often only two-thirds as great;

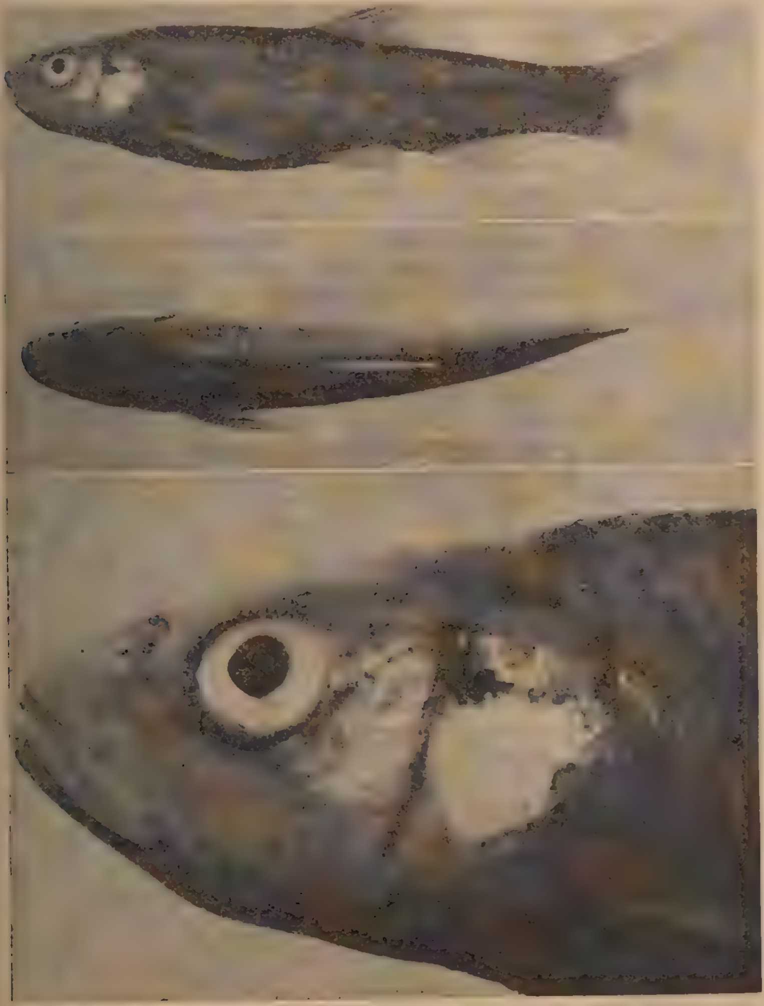

Plate III

Fig. 1. *Notropis potteri*: lateral view of an adult paratype 66 mm. long, collected in Brazos River at Government Dam, Texas, by Kelshaw Bonham, on December 3, 1939.

Fig. 2. *Notropis potteri*: dorsal view of a 62 mm. paratype from the same collection.

Fig. 3. *Notropis potteri*: enlarged view of the head of specimen shown in Fig. 1.

the caudal is usually a little shorter than the head; the pectoral length about equals the dorsal height; the pectoral does not reach the pelvic insertion. The dorsal origin is near or a little behind the middle of the standard length, approximately over the pelvic insertion.

The body contours are symmetrically curved, with most of the small eye above the axis. The muzzle is very thick and blunt in side view, with the heavy jaws about equal in forward projection. The snout in top view is extremely massive, almost semicircular. The mouth is moderately oblique: the upper lip rises to the level through the lower margin or the lower part of the pupil (Pl. III, Fig. 3). The middle part of the lower lip and the posterior part of the upper lip are much swollen.

The complete lateral line is nearly straight, horizontal, and median behind the short downward anterior curve. Its scales are scarcely modified in outline.

The body is moderately dusky above and silvery below, with little pigment below the region of the lateral line. The melanophores on the upper parts of the head and body are rather evenly scattered. Large melanophores are dispersed about the lateral line anteriorly. The lateral dark band is moderately developed on the caudal peduncle and ends just in advance of the very weak and diffuse basicaudal spot.

COMPARISONS.—*Notropis potteri* is one of the more distinctive of the many species that constitute the genus. The broad head, heavy muzzle and big mouth, well shown in the figures (Pl. III), accord it an aspect surprisingly like that of the creek chub, *Semotilus atromaculatus*. In some respects it shares characters with the Gulf-coastal species *N. sabinae* Jordan and Gilbert, but it is a much larger and coarser fish, with a somewhat smaller and much less inferior and less horizontal mouth. It also shows some resemblance to *N. bairdi* and *N. girardi* Hubbs and Ortenburger (1929*a*: 29-33), which seem to represent *N. sabinae* in the Red and Arkansas river systems, respectively. Since it differs from *sabinae, bairdi* and *girardi* in the dental formula, its resemblance to those species is probably not indicative of very close relationship.

Except for the consistent development of a second row of two pharyngeal teeth and for the complete squamation of the nape and breast, the specimens of *N. potteri* scarcely differ from the original account of *N. bairdi* and agree strikingly in some respects, for example in the superficial resemblance to *Semotilus atromaculatus*. On comparing *potteri* with the types of *bairdi*, however, close attention to detail discloses numerous other trenchant differences. The pharyngeal arch is less heavy (items 3 and 4 in the accompanying comparison); the scales are larger, are shield-shaped instead of suboval, and have fewer radii (items 6-8). The skin is thinner and less papillose (9). The body is slenderer, especially in adult females (10). The head is notably slenderer and thinner and the margins are straightish rather than notably turgid (12-14). The mouth and lip structures are very different (15-21). The opercle is much smaller (22). There are also sharp differences in pigmentation (24-29).

The relationship is probably more intimate with *Notropis blennius* (Girard), the status of which was clarified by Fowler (1910: 274-276, figs. 4, 6, 10) and by Hubbs (1926: 42-44). When compared with either of the subspecies into which *N. blennius* now seems divisible, *N. potteri* stands out so sharply as to call for full specific separation.

The subspecies of *blennius* may be called *Notropis blennius blennius* (Girard) and *N. b. jejunus* (Forbes). Specimens from the Arkansas River in Oklahoma are topotypic of *Alburnops blennius* Girard (1856: 194; 1858: 261, pl. 57, figs. 13-16 referred to but not bound in same volume; 1859: 55, pl. 57, figs. 13-16). They agree with Girard's description and figure in some important respects, such as the deep and abruptly decurved snout and low mouth. Adequate material from the Cimarron River and from various smaller tributaries also represents the nominate subspecies. The same form occurs in the Arkansas and Missouri rivers in Kansas. A specimen collected by George A. Moore and J. M. Paden in the Red River system, in Bricken Spring, 24 miles south of Ada, Oklahoma, on April 5, 1947, is typical of *N. b. blennius*, but is thought by Dr. Moore to represent a bait introduction, as it was taken on the premises of Thomas Bricken, a bait dealer, who gets his material from the Arkansas River system as well as the Red. As determined by reexamination of the collections in the University of Michigan Museum of Zoology, *N. b. jejunus* ranges from the Plains streams of Alberta and Manitoba in Canada through the Red River and Mississippi River of Minnesota and through the Mississippi River drainage basin of Iowa, Illinois, Indiana, Ohio, Kentucky, Tennessee and Missouri to the Mississippi River in Arkansas. It also occurs in the Tombigbee River in Alabama. The Neosho and Illinois rivers in Oklahoma, which are clearer and cooler than other streams in the same region, are inhabited by the northern subspecies. Since the differential characters of the two forms, outlined below, show moderate overlap and some degree of both local and individual inconsistency, and especially since the abundant material from Nebraska exhibits varying degrees of intermediacy and of mixture of characters, only subspecific separation is justified, and until the material is more critically analyzed and until the differences can be demonstrated to be genetic, even the subspecific separation must be regarded as tentative.

Since this paper was written the pertinence of the name *blennius* to the form here called *N. b. blennius* was confirmed at the National Museum by an examination of the type series (No. 67). The 6 largest specimens, 51 to 65 mm. long, including one of 56 mm. labelled "Type" in Jordan's handwriting, agree with the type figure, and are *N. b. blennius*. They have the deep head, decurved snout, low mouth, small eye, and most other characters here attributed to the typical subspecies, but not the small scale size (the total length of the key scale enters the postorbital length 2.7 to 3.0 times). The 5 smaller types, 38 to 44 mm. long, represent the unnamed creek subspecies of *Notropis volucella* Cope which inhabits the Neocho River system and other waters in the contiguous parts of Oklahoma, Arkansas, Missouri, and Kansas and which is characterized by the only moderate elevation of the lateral-line scales, the smallish size, the large eye, the high dorsal fin and the chunky body. These 5 specimens have been recataloged as U.S.N.M. 152780. Their characters were apparently not considered in the preparation of the type figure and description of *Alburnops blennius*.

N. b. blennius differs from *N. b. jejunus* in the usually less flattened and less expansive upper limb of the pharyngeal arch (item 3 in accompanying comparison of forms); the somewhat smaller rather less shield-shaped scales, the length of the median scales entering the postorbital more instead of less than 3.0 times (items 6-7), with slight overlap in some series; the somewhat thicker and more papillose skin (9); the deeper body, with more arched anterodorsal profile (10); the usually deeper and wider head (12-13); the usually more nearly horizontal mouth and the blunter and more decurved snout (15-16); on the average probably in the somewhat thicker lips (17-19), and shorter mouth (21); usually in the longer opercle (22) and smaller eye (23); and somewhat in the pigmentation (26-29).

The differences between *potteri* and both forms of *blennius*, as here recognized, are also outlined in the accompanying comparison. The teeth of the second row are stronger, less deciduous, and more constantly developed (items 1-2). The pharyngeal arches are relatively larger than in either form (4) and the upper limb is more rodlike, less flangelike, particularly in comparison with *jejunus* (3). The ratio between scale length and postorbital contrasts with that of *blennius* (6) and the scale is usually more shield-shaped, less suboval, than in that subspecies (7). The radii average more (item 8). The skin seems smoother and less coarsely papillose than in *N. b. blennius* (9). The body averages slenderer than in that subspecies (10). The head averages slightly longer (11) and definitely slenderer (12). Its margins are less curved than in *N. b. blennius* (14). The mouth averages more oblique and higher anteriorly than in that subspecies (15-16). The local thickening of the lips and the resulting sigmoid gape give the mouth of *potteri* a strikingly different physiognomy, although *N. b. blennius* sometimes slightly approaches *potteri* in these respects (17-20). The opercle is usually smaller, especially in comparison with *N. b. blennius* (22). The eye averages smaller than in that subspecies and at comparable sizes is definitely smaller than in *jejunus* (23).

COMPARISON OF *Notropis potteri* WITH SIMILAR FORMS

1. *Pharyngeal tooth formula*:
    - *N. potteri*: 2, 4—4, 2.
    - *N. bairdi*: 4—4 (5—4 in 1 specimen, with the 5 on the left side normal in appearance).
    - *N. blennius*, both subspecies: 1 or 2, 4—4, 1 or 2.
2. *Teeth of lesser row:*
    - *N. potteri*: large, strong, firmly fixed; both constantly present.
    - *N. bairdi*: consistently absent; the arch rather swollen in their place, not flattened as in the 3 other forms.
    - *N. blennius blennius*: small and very weak, not very firmly fixed, one frequently lost and occasionally never developed.
    - *N. blennius jejunus*: as in *blennius blennius*, but perhaps not quite so weak.
3. *Pharyngeal arch:*
    - *N. potteri*: only moderately heavy; upper limb usually more or less rodlike, approaching lower limb in form.
    - *N. bairdi*: much heavier than in the 3 other forms.
    - *N. blennius blennius*: weakest; in form of arch about intermediate between *potteri* and *jejunus*.
    - *N. blennius jejunus*: averaging weaker than in *potteri;* upper limb usually a thin, broad flange.
4. *Width across both arches, laid with ends together on a flat surface, stepped into head length:*
    - *N. potteri*: 2.3 to 2.5, rarely 2.6.

N. bairdi: 1.9 to 2.2.
N. blennius blennius: 2.5 (rarely) to 2.7.
N. blennius jejunus: 2.4 to 2.7.

5. *Squamation on nape and on breast:*
   N. potteri, N. blennius blennius and *N. blennius jejunus*: complete.
   N. bairdi: usually incomplete, with scaleless area small to large.
6. *Median horizontal length of entire scale from first row above lateral line, below dorsal fin, measured into postorbital:*
   N. potteri: more than 3.0 but less than 4.0 times.
   N. bairdi: more than 4.0 times (reflecting the long opercle and the small eye as well as the small scales).
   N. blennius blennius: usually between 3.0 and 4.0 times, occasionally slightly less than 3.0 times.
   N. blennius jejunus: typically less than 3.0 times, sometimes slightly more than 3.0 times (reflecting larger scale and larger eye).
7. *Shape of scales from near middle of sides:*
   N. potteri: strongly shield-shaped, with prominent anterior angles in outline and in course of circuli; posterior margin somewhat produced.
   N. bairdi: suboval, with very weak anterior angles and scarcely produced posterior margin.
   N. blennius blennius: somewhat shield-shaped (intermediate between *bairdi* and 2 other forms).
   N. blennius jejunus: about as in *potteri.*
8. *Radii:*
   N. potteri: rather few.
   N. bairdi: rather numerous.
   N. blennius, both subspecies: very few.
9. *Skin texture:*
   N. potteri: rather thin and smooth, with microscopic papillae.
   N. bairdi: thick and tough with coarse papillae.
   N. blennius blennius: intermediate between *bairdi* and the 2 other forms.
   N. blennius jejunus: about as in *potteri.*
10. *Greatest depth of body in standard length* (these differences are accentuated when specimens of the same sex and of similar size are compared):
    N. potteri: 3.7 to 4.8 (average of 40, 4.26).
    N. bairdi: 3.6 to 4.5 (average of 37, 4.00).
    N. blennius blennius: 3.7 to 4.3 (average of 17, 3.92); as a result of the deep body and the low mouth, the anterior dorsal profile is typically more arched than in *N. b. jejunus.*
    N. blennius jejunus: 4.0 to 4.8 (average of 43, 4.39).
11. *Head length stepped into standard length* (these differences are accentuated when specimens of like size are compared):
    N. potteri: 3.3 to 3.8 (average of 61, 3.56).
    N. bairdi: 3.3 to 3.8 (average of 30, 3.63).
    N. blennius blennius: 3.4 to 4.1 (average of 17, 3.69).
    N. blennius jejunus: 3.7 to 4.0 (average of 32, 3.77).
12. *Head depth stepped into head length:*
    N. potteri: 1.65 to 1.8.

   N. bairdi: 1.5 to 1.65.
   N. blennius blennius: 1.4 to 1.6, usually 1.5.
   N. blennius jejunus: 1.5 to 1.75, usually 1.6 to 1.7.

13. *Head width stepped into head length:*
   N. potteri: 1.7 to 2.0.
   N. bairdi: 1.5 to 1.7.
   N. blennius blennius: 1.6 to 1.9, usually 1.7 to 1.8.
   N. blennius jejunus: 1.7 to 2.0, usually 1.8 to 1.9.
14. *Head margins:*
   N. potteri: straightish, even in large adults.
   N. bairdi: more strongly curved, becoming extremely turgid in large adults.
   N. blennius blennius: somewhat approaching *bairdi.*
   N. blennius jejunus: almost as straight as in *potteri.*
15. *Mouth:*
   N. potteri, N. bairdi (usually) and *N. blennius jejunus*: moderately oblique.
   N. blennius blennius: subhorizontal to moderately oblique.
16. *Horizontal from front of rostral fold crossing orbit at:*
   N. potteri: lower margin or lower part of pupil.
   N. bairdi: variable, from lower margin of orbit to lower part of pupil.
   N. blennius blennius: lower margin of orbit or a little higher (in correlation, the snout is blunter and more decurved than in the 3 other forms).
   N. blennius jejunus: usually about midway between lower margin of orbit and lower edge of pupil.
17. *Upper lip:*
   N. potteri: markedly dilated and swollen posteriorly.
   N. bairdi: scarcely dilated, thin throughout.
   N. blennius blennius: thin throughout to slightly thickened posteriorly.
   N. blennius jejunus: scarcely dilated.
18. *Lower lip:*
   N. potteri: markedly dilated medially.
   N. bairdi: scarcely dilated, thin throughout.
   N. blennius blennius: thin throughout to slightly thickened medially.
   N. blennius jejunus: scarcely dilated.
19. *Shape of gape (resulting from degree of thickening of lips):*
   N. potteri: rather strongly sigmoid.
   N. bairdi and *N. blennius jejunus*: scarcely sigmoid.
   N. blennius blennius: straight to slightly sigmoid.
20. *Length of conjoined lip behind end of gape, compared with length of pupil:*
   N. potteri: nearly or quite as long.
   N. bairdi and both subspecies of *N. blennius*: about one-half as long.
21. *End of gape approximately under:*
   N. potteri: posterior nostril.
   N. bairdi and *N. blennius jejunus*: front of orbit.
   N. blennius blennius: intermediate.
22. *Length of opercle (from extreme tip of membrane to nearest point on preopercular margin) stepped into greatest distance from tip of snout*

to preopercular margin:
N. potteri: 2.2 to 2.7, usually 2.3 to 2.5.
N. bairdi: 1.7 to 2.0.
N. blennius blennius: 1.85 to 2.45, usually 2.0 to 2.3.
N. blennius jejunus: 2.1 to 2.6, usually 2.2 to 2.4.

23. *Length of eye (cornea) stepped into length of head* (these differences are accentuated when specimens of like size are compared; toward the far north the eye in *jejunus* becomes reduced):
N. potteri: 4.2 to 5.5 (average of 61, 4.72).
N. bairdi: 4.4 to 5.6 (average of 30, 5.02).
N. blennius blennius: 4.2 to 5.4 (average of 17, 4.57).
N. blennius jejunus: 3.6 to 4.4 (average of 32, 3.97).

24. *Pigment along base of dorsal fin:*
N. potteri and both subspecies of *N. blennius*: fin base rather evenly bordered by mid-dorsal dark streak.
N. bairdi: middle of base blackened; front and end of base more or less completely depigmented.

25. *Narrow dark streak above main lateral dark band:*
N. potteri and both subspecies of *N. blennius*: scarcely diffentiated from main band.
N. bairdi: sharply set off from main band, with an intervening scarcely pigmented area, especially in half-grown (in young pigment may be poorly developed; in adult pigment may be more uniformly distributed).

26. *Pigment on scale row below lateral line on anterior part of trunk:*
N. potteri: undeveloped.
N. bairdi: well developed in adult.
N. blennius blennius: undeveloped to moderately developed.
N. blennius jejunus: moderately to well developed.

27. *Pigment on cheek below horizontal from just below orbit:*
N. potteri: scarcely developed onto cheek, ending below front nostril.
N. bairdi: developed down to or nearly to rostral rim and back to behind vertical from front of eye.
N. blennius, both subspecies: developed down to or nearly to rostral rim and back to below vertical from posterior nostril.

28. *Pigment on upper lip:*
N. potteri: usually moderately well developed, at least anteriorly.
N. bairdi: lacking to weakly developed, anteriorly.
N. blennius blennius: moderately to well developed.
N. blennius jejunus: well developed.

29. *Pigment on lower lip:*
N. potteri: usually weakly developed, at front.
N. bairdi: lacking or barely developed.
N. blennius blennius: usually weakly developed.
N. blennius jejunus: weakly to moderately developed.

RANGE AND HABITAT.—*Notropis potteri* occurs not only in the silty Brazos River and its main tributaries, along with *oxyrhynchus* and *brazosensis*, but also in some of the smaller and less turbid waters of this river system. As a native fish it seems to be confined to the Brazos system. It has recently been taken in the Red River system, but we think it probable that the population there has become established from escaped bait minnows, originally from the Brazos River system. No specimens were recognized among the myriads of fish from the Red River and tributaries collected in 1925, 1926 and 1927 (reported by Ortenburger and Hubbs, 1927, and by Hubbs and Ortenburger, 1929*a-b*), nor in other, unreported collections from those waters made prior to 1948. The material in the University of Michigan Museum of Zoology, comprising more than 1,800 specimens collected in 1926 and smaller numbers taken in 1925, 1929, and 1932, was all carefully reexamined in this connection. The specimens taken in 1948 and 1949 were from Lake Texoma, a heavily fished artificial lake, and the Red River, mostly near the lake. Those from the lake were collected by Frank T. Knapp on June 25, 1949, at Burns Run Resort, Bryan County, Oklahoma, near highway 75A. Series from the river below the lake were seined north of Paris, Lamar County, Texas, by George A. Moore and party on March 28, 1948, and by Knapp and party on July 8, 1949, and south of Yuba, Bryan County, Oklahoma, on Highway 299, by Moore and class on March 15, 1949. Four were seined by Knapp and party on June 23, 1949, in the Red River far above the lake, at Davidson, Tillman County, Oklahoma. No specimens have been identified in collections from the Trinity or other river systems between the Brazos and the Red. Comparison of specimens shows no notable difference. The tabulated proportional measurements (Table VI) are very similar, considering the difference in habitat, the difference in average size of specimens, and the fact that the Brazos and Red specimens were measured by different men. The biggest indicated difference in proportions, in head length, was not verified in measuring larger series of specimens for the preceding species comparison.

TYPES.—The holotype (University of Michigan Museum of Zoology, No. 120228), an adult 45.3 mm. in standard length, was seined by the Hubbs family and Leo T. Murray in Waco Creek, McLennan County, Texas, on June 21, 1938. The paratypes were taken with the holotype and at several other places in the Brazos River system. The 22 paratypes measured for Table VI were collected with the holotype; and in Brazos River at Government Dam, near Navasota, on November 24, 1939, by Bonham and party; in Little Brazos River at State Highway 21, on June 13 and July 13, 1940, by Bonham and party; at the Texas state fish hatchery at Cisco (received August 24, 1936, from George E. Potter); and in the lower end of Toweash Creek, a Brazos River tributary, by Marion Toole. Other paratypes were collected by G. E. Potter in Waco Creek, Baylor University Campus, Waco, on March 3, 1931, in Baylor Creek, at Waco, on January 22, 1931, and in unspecified waters at Waco; by R. T. Richey in Little Brazos River, Brazos County, on March 23, 1936, and at an unspecified locality and date in the Brazos River system; and by Bonham and students in Brazos River at Government Dam, on December 3, 1939. Specimens not designated as paratypes were taken by Bonham and students in Brazos River at Wellborn Crossing, Brazos County, on October 31, 1931, and in Little Brazos River, Brazos County, on March 31, 1939.

Subsequent to the preparation of the diagnosis other specimens, not designated as paratypes, have been collected by Frank T. Knapp of the Agricultural and Mechanical College of Texas and by Clark Hubbs of the University of Texas.

This species is dedicated to an enthusiastic naturalist, Dr. George E. Potter, formerly of Baylor University and now at the Agricultural and

Mechanical College of Texas. He collected the first specimens of the species and submitted them to the senior author for study.

SUMMARY

Among the many new fishes added during the past three decades to the known freshwater fish fauna of eastern North America are the three now belatedly described from eastern Texas—*Notropis oxyrhynchus*, *N. brazosensis*, and *N. potteri*. These species characterize the larger silty streams of the Brazos River system, which are thus shown to have a somewhat distinctive fauna. *N. oxyrhynchus* and *N. potteri* appear to be confined to this system (a population of *potteri* in the Red River system is thought to be the result of bait-minnow introduction); *N. brazosensis* occurs also in the lower parts of adjacent river systems. *N. potteri* also inhabits smaller and clearer streams.

TABLE VI

MEASUREMENTS (IN THOUSANDTHS OF STANDARD LENGTH) AND COUNTS OF TYPES OF *Notropis potteri*

The types were measured by Kelshaw Bonham, the Red River specimens by Frank T. Knapp.

	Holotype	22 Paratypes (Range and Mean)	19 from Red River (Range and Mean)
Standard length, mm.	45 3	38.7—80.0 (48.7)	34.2—64.3 (44.2)
Predorsal length	523	497—567 (527)	500—543 (521)
Prepelvic length	505	511—552 (528)	491—548 (517)
Body depth	245	211—263 (233)	210—265 (228)
Dorsal origin to lateral line	153	126—159 (141)	119—159 (131)
Pelvic insertion to lateral line	120	80—123 (97)	83—127 (100)
Body width	181	152—191 (170)	125—195 (163)
Caudal peduncle length	221	183—231 (203)	183—240 (221)
Caudal peduncle depth	117	105—124 (113)	106—125 (114)
Head length	297	267—318 (301)	252—294 (278)
Head depth	180	161—195 (177)	156—182 (167)
Snout length	83	85—104 (95)	73—93 (85)
Eye length	66	49—66 (58)	50—69 (60)
Fleshy interorbital	100	93—128 (105)	87—107 (95)
Upper jaw length	86	86—110 (98)	94—112 (101)
Mouth width [1]	72	71—109 (86)	74—93 (82)
Dorsal height	240	209—243 (229)	199—244 (225)
Anal height	172	159—188 (171)	159—190 (172)
Anal base	81	82—104 (91)	79—108 (91)
Longest caudal ray	300	255—314 (281)	251—326 (272)
Pectoral length	253	195—253 (221)	188—244 (211)
Pelvic length	158	143—169 (155)	137—168 (149)
Scales			
Above lateral line	6	5—6 (5.72)	6—7 (6.16)
Along lateral line	35	34—37 (35.0)	34—36 (34.6)
Below lateral line	4	4—5 (4.52)	4—5 (4.32)
Lateral line to pelvic	4	3—5 (4.52)	4—4 (4.00)
Predorsal scales	19	15—24 (19.1)	16—20 (18.1)[2]
Predorsal rows	15	13—18 (15.3)	14—17 (15.8)
Around body: Above	13	11—14 (12.6)	11—13 (11.9)
Below	13	12—16 (13.9)	11—14 (12.5)
Total	28	25—31 (28.4)	24—28 (25.8)
Around caudal peduncle: Above	6	5—7 (5.91)	5—6 (5.53)
Below	5	5—8 (5.52)	5—6 (5.11)
Total	13	12—16 (13.4)	12—13 (12.6)
Fin Rays			
Dorsal	8	8—8 (8.00)	7—8 (7.95)
Anal (Table I)	7	7—8 (7.04)	6—8 (7.00)
Pectoral	16—16	14—18 (15.7)[3]	13—16 (14.9)[3]
Pelvic	8—8	8—9 (8.07)[3]	7—8 (7.97)[3]

[1] Between ends of gape.
[2] 18 specimens.
[3] Both sides counted.

Notropis oxyrhynchus appears to be the southwestern representative of *N. percobromus,* the status of which is further elucidated. *N. brazosensis* seems to represent *N. illecebrosa. N. potteri* resembles *N. Sabinae, N. bairdi,* and *N. girardi,* but is probably more closely related to *N. blennius,* which is held to comprise two subspecies, *N. b. blennius* of the generally silty Southwestern streams, especially of the Arkansas River system, and *N. b. jejunus* of more northern and more eastern waters. Detailed comparisons are made between *oxyrhynchus* and *percobromus,* between *brazosensis* and *illecebrosa,* and between *potteri, bairdi,* and the two subspecies of *blennius.*

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Reprinted from
THE TEXAS JOURNAL OF SCIENCE
Volume 3, Number 1

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Scripps Institution of Oceanography, Bull., Tech. ser., v. 6:2.

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Odontoscion australis, the Juvenile Stage of *Elattarchus archidium*, a Panamaic Sciaenid Fish

Carl L. Hubbs and Boyd W. Walker

Reprinted from Copeia, 1951, No. 3, August 31

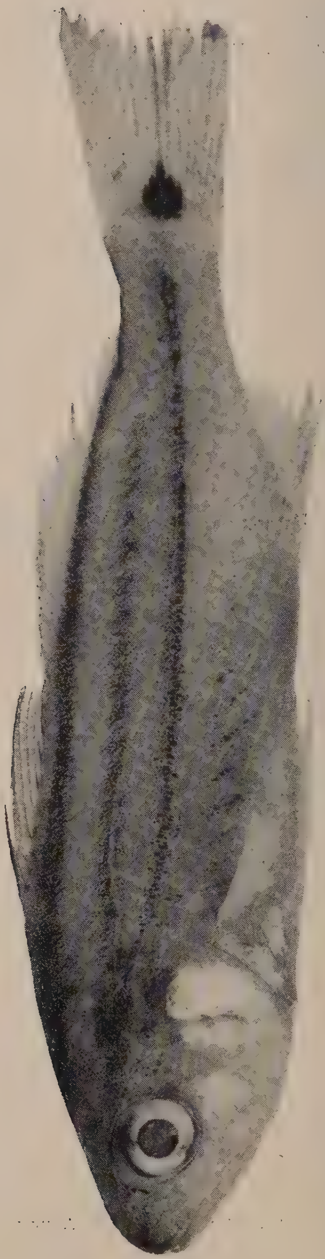

Fig. 1. Juvenile *Elattarchus archidium*, representing stage described from Perú as *Odontoscion australis*. Specimen 59 mm. in standard length collected at San Carlos Bay, Gulf of California on February 1, 1950. Photographed by John B. MacFall.

Odontoscion australis, the Juvenile Stage of *Elattarchus archidium*, a Panamaic Sciaenid Fish[1]

Carl L. Hubbs and Boyd W. Walker

URING the identification by the junior author of large series of croakers (Sciaenidae) recently collected in the Gulf of California, certain ng specimens (Fig. 1) were encountered that correspond very closely with original description and figure of *Odontoscion australis*, described by lebrand (1946: 280–82, fig. 59) from Perú. Except for their boldly ed color pattern, in which respect they resemble the juvenile stage of ain other sciaenids, for example *Cheilotrema saturnum* (Girard) of Calia, these Gulf specimens also agree well with the descriptions of *Elattars archidium* (Jordan and Gilbert). That species was described as *Odonion archidium* by Jordan and Gilbert (1882: 316–18) and was referred *airdiella* by Jordan and Eigenmann (1899: 383–86) and to *Corvina* by lenger (1899: 4). It has long been placed in a monotypic genus under name *Elattarchus archidium* (Jordan and Evermann, 1898: 1431–32; ert and Starks, 1904: 125–26; Meek and Hildebrand, 1925: 628–29). ounts and measurements the Gulf specimens agree satisfactorily with both inal species and in the diagnostic canine dentition they correspond with detailed description of *E. archidium* by Gilbert and Starks.

Elattarchus archidium is one of the many endemic species and represents of the several endemic genera in the outstandingly rich sciaenid fauna of Panamaic region. It has been recorded from San Juan Lagoon, near ymas, Gulf of California (Gilbert and Starks, 1904: 126) to Ecuador ulenger, 1899: 4).

Several small series of specimens were collected from January 29 to Feby 1, 1950, in the Gulf of California along the coast of Sonora, México, the junior author and his assistant Arthur O. Flechsig, with the aid of id Joseph, Kenneth S. Norris and Andreas B. Rechnitzer, students of the ors. Data follow: collection W50-20, Miramar Beach on Bocochibampo , near Guaymas, Lat. 27° 55′ 07″ N., Long. 110° 58′ 22″ W., 1 yearling mm. in standard length; W50-36, sand beach about 1 mile east of San los Bay, near Guaymas, Lat. 57° 56′ 50″ N., Long. 110° 04′ 35″ W., 8 rlings, 53-66 mm. long; W50-43, vicinity of Boca del Río Mayo, Lat. 40′ N., Long. 109° 47′ W., 2 half-grown 107-109 mm. long; W50-47 W50-49, San Carlos Bay, Lat 27° 57′ 10″ N., Long. 111° 05′ 35″ W., 2 rlings, 59-63 mm. long.

After comparing our young specimens from the Gulf of California with references cited above, we concluded that *Odontoscion australis* was ably based on the young of *Elattarchus archidium*. This conclusion was fied by the senior author at the United States National Museum. With active and friendly cooperation of Leonard P. Schultz, curator of fishes, types of the two nominal species were examined, along with other critical imens from Panamá.

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[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 505.

The adult stage, of plain coloration and with the lowermost preopercul spine much enlarged and abruptly downcurved posteriorly, is represente in the National Museum by 2 cotypes of *O. archidium* from Panamá—USN No. 29266, 152 mm. in standard length, and No. 29518, 162 mm. lon Three very similar specimens, No. 50404, 151-159 mm. long, were also co lected by Gilbert at Panamá, but were not designated as cotypes.

The juvenile stage (Fig. 1), with bold stripes and with the lowermost pr opercular spine still directed more backward than downward and not y greatly enlarged, is represented in the National Museum by 4 types of *australis* seined from Lobos de Tierra Bay, Perú, at Lat. 06° 26′ S., Lon 80° 51′ W., by M. J. Lobell on May 7, 1941. The holotype, USNM N 128023, measures 66 mm. in standard length; the 3 paratypes, No. 12802 60, 71 and 73 mm.

The juvenile color pattern of *E. archidium* (Fig. 1) is not very accurate shown in the type figure of *O. australis*. The dorsolateral stripe was draw with a strong downward curve, so that it wrongly appears to approach t median band, whereas in the specimens these parallel bands remain appro mately equidistant. Furthermore, the bands and the caudal spot are show too weak and the dorsal stripe is not sharply indicated.

The connection between the juvenile (*australis*) and the adult (*arch dium*) phases is clearly demonstrated by additional specimens collected ne Panamá in 1935 and 1937. One young of 36 mm., USNM No. 144651, co lected on Pedro Gonzales Island of the Pearl Islands by Samuel F. Hildebra on March 1, 1935, shows in simplified form the coloration of the types *O. australis*. There is no indication along the lateral line of the forward directed spur of the median stripe, where the lateral line rises above t stripe, and no trace of the short broken stripe that is also developed in larg young on the lower anterior side. The 3 primary stripes are bold, as is al the large dark spot on the caudal base. Two half-grown, USNM No. 14465 120 and 127 mm. long, from Panamá Bay, preserved in March, 1937 by M Whaler for S. F. Hildebrand, show fading traces of the lateral stripes a the caudal spot of the young, but have already developed a long, stron downturned lower preopercular spine. In 2 specimens of intermediate si 107-109 mm. long, from near Boca del Río Mayo, Sonora, México, the lowe most spine is considerably strengthened but is downcurved only near t tip. Close scrutiny, however, shows that the spine in the half-grown a adult specimens has a subhorizontal base. These observations indicate th the spine is originally oriented at a down-sloping angle of only about 3 and that it becomes strengthened and abruptly bent downward to an angle 90° or more with the horizontal as the fish transforms from the juvenile the subadult phase. The study of these series eliminated all remaining dou concerning the pertinence of *O. australis* to *E. archidium.*

The preopercular spines in the types of *O. australis* negate its referen to *Odontoscion,* even though the spines are still rather small and are larg covered by membrane in well-preserved specimens like the types, and ev though the lowermost spine has not yet become greatly enlarged and dow curved. In addition to the few spines, which are similarly characteristic *Bairdiella,* the preopercular margin in the young *E. archidium* also bea erous sharp though soft points, like those of *Odontoscion.* Such points, no true spines, are borne on the preopercular margin of *O. xanthops,* as sented by 3 adults (USNM Nos. 80762–64) collected at Panamá by k and Hildebrand. The relationship between *E. archidium* and *O. xan-* *s* appears to be much less intimate than is suggested by Hildebrand's arison (1946: 282).

o conclude: *"Odontoscion australis"* is merely the juvenile stage and a nym of *Elattarchus archidium,* one of the endemic elements in the rich nid fauna of the Panamaic region.

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IPPS INSTITUTION OF OCEANOGRAPHY, LA JOLLA, CALIF., AND DEPT. OF ZOOLOGY, UNIV. OF CALIFORNIA, LOS ANGELES 24, CALIF.

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REPRINT FROM

CALIFORNIA FISH and GAME

"CONSERVATION OF WILDLIFE THROUGH EDUCATION"

VOLUME 37 SAN FRANCISCO, APRIL, 1951 NUMBER 2

TOXICITY OF THE ROE OF THE CABEZON, *SCORPAENICHTHYS MARMORATUS*[1]

By CARL L. HUBBS and ARNE N. WICK
Scripps Institution of Oceanography (University of
California) and Scripps Metabolic Clinic

An unhappy gastronomic experience of the senior author and his wife and laboratory experiments by the junior author indicate rather definitely that there is some toxic constituent in the roe of the cabezon, *Scorpaenichthys marmoratus* Girard, a large cottid fish of western North America.

On January 14, 1923, a ripe adult female cabezon, 440 mm. in standard length, caught during the day in a tidepool on Point Lobos, Monterey County, California, was eaten for supper. The senior author and his wife partook of the roe while her parents and a young child ate the flesh. Those who ate the flesh were not discomforted in the least, nor have we heard of anyone having been poisoned by eating this common food and game fish. The two who ate the eggs awoke in misery about four hours afterward and were violently ill throughout the rest of the night, with rapidly alternating chills and fever and with frequent vomiting and diarrhea. There was, however, no marked prostration, fainting, dizziness, or paralysis. Both were left very weak in the morning but gradually recovered during the day, with no residual or recurrent symptoms. No medical attention was received.

This experience, related to fellow ichthyologists, was the basis for the statement by Walford (1931, p. 127), that "although the flesh is of excellent quality the roe is said to be poisonous," and for the following remarks by Schultz (1948, p. 68):

> "Also, it is definitely known that the eggs of certain fishes are poisonous, although the fishes themselves are not. (Dr. Hubbs became very sick after eating some eggs of a United States Pacific Coast marine sculpin.)"

When a very large female collected at the Scripps Institution reef by Jack Prodanovich on December 23, 1949, was found to be full of nearly-ripe roe, a long desire for an experimental test of the toxicity of the roe was reactivated. The ovaries were promptly hard-frozen. They were kept in that condition for nine months, until the experiments were run.

The experimental results (Table 1) confirmed the experience recounted above. A portion of the roe (77 g.) and 50 ml. of water were homogenized for five minutes in a Waring Blendor. The mixture was fed orally to 12 male albino rats and to two guinea pigs. The animals had in addition their regular food at all times. Four rats and one guinea pig

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[1] Contribution from the Scripps Institution of Oceanography, New Series, No. 506, and from the Scripps Metabolic Clinic. Submitted for publication, November, 1950.

TABLE 1

Data on Toxicity of Cabezon Roe to Rats and Guinea Pigs

Animal	Weight of animal	Weight of roe administered		Death time (hrs.)
		Grams	Percent body wt.	
Rat	330	7.7	2.33	22
	420	7.7	1.83	22
	272	1.43	0.53	84
	291	1.43	0.49	--
	314	1.07	0.34	--
	318	1.07	0.34	--
	326	0.71	0.22	76
	343	0.71	0.21	--
	292	0.36	0.12	--
	302	0.36	0.12	--
	338	0.18	0.05	--
	350	0.18	0.05	--
Guinea Pig	355	1.43	0.04	30
	400	1.43	0.36	--

died. All the animals exhibited diarrhea and nasal discharge, but these conditions diminished in intensity as the dose was decreased.

It would obviously be unwise to eat the roe of the cabezon, but there is no indication that the flesh of this fish is in any way harmful.

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n *United States of America*
rom THE SCIENTIFIC MONTHLY
LXII, No. 6, June, 1951

he Pacific Sardine sappearing?

J. L. McHUGH* and ELBERT H. AHLSTROM†

The senior author, a native of British Columbia, completed his doctoral research in 1950 at the Scripps Institution, where he has most recently been associated with the investigation of the sardine, a part of the Marine Life Research program. Previously he was a scientific assistant of the Fisheries Research Board of Canada until he was called into military service. In January 1951 he became director of the Virginia Fisheries Laboratory. Dr. Ahlstrom (Ph.D., Ohio State, 1934) has been with the Fish and Wildlife Service since 1939, and is now in charge of the recruitment research on the California sardine. He is concerned also with the identification of the fish larvae occurring off the west coast of North America and has been successful in tracing a number of complicated life histories.

CHING a maximum of almost 800,000
ons in the season of 1936–37 and remain-
ig above the half-million-ton level during
ig eight seasons, the annual catch of sar-
ng the Pacific coast of North America
abruptly in the years following 1945. So
s this drop that by 1947–48 the total
only slightly exceeded 100,000 tons.
by the disaster that appeared to be
ng this major California industry, which
about 90 per cent of the total Pacific
dine catch, the fishery operators began to
he research being conducted.

valuable research on the sardine had been
l was in progress at the time of the
out the work was hampered by a lack of
funds and facilities. Both scientists and
felt the need of expanding the research
pecially in the oceanographic field.

the spring of 1946 the San Francisco
ssociation allotted $30,000 for an inves-
of availability of sardines off San Fran-
he purse seine vessel *Pearl Harbor,*
with echo-ranging gear as an aid in lo-
rdine schools, made a number of cruises
l California. Scientists of the California
of Fish and Game and the U. S. Fish and
Service who participated in these cruises
servations on temperature and plankton
distribution. Only limited information was secured on sardine availability, but the industry was impressed with the value of oceanographic fisheries research, notwithstanding its high cost.

To provide additional research funds the California sardine operators in 1947 voluntarily proposed a levy of 50 cents per ton on sardine landings, in addition to a similar tax then in effect. A Marine Research Committee, consisting of nine members representing the industry, scientists, and the people of California, was set up to administer the new funds. This body was largely responsible for securing from the California legislature a grant of $300,000 (later about $400,000) annually to the University of California for marine life research, with particular emphasis on the analysis of oceanographic conditions that may determine the productivity of the ocean waters.

The augmented sardine research program is a unique cooperative venture in oceanography and fisheries biology. Major contributions are being made by the Bureau of Marine Fisheries of the California Division of Fish and Game, the South Pacific Fishery Investigations of the U. S. Fish and Wildlife Service, and the Scripps Institution of Oceanography of the University of California. In addition, the California Academy of Sciences is studying sardine behavior.

The work at sea, which forms so important a part of the expanded program, requires a fleet of vessels capable of cruising the open Pacific and carrying out their duties under almost all weather conditions. For this purpose, four ships are en-

bution from the Scripps Institution of Ocea-
New Series, No. 508.
hed by permission of the Director, U. S. Fish
ife Service.

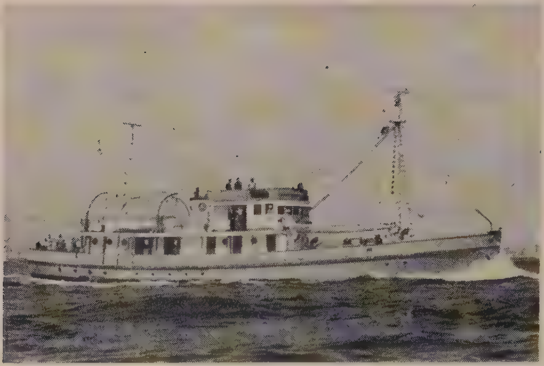


FIG. 1. The *Yellowfin,* research vessel of the Bureau of Marine Fisheries, California Division of Fish and Game, engaged mostly on studies of the Pacific sardine.

gaged exclusively in the collection of data. These are the *Yellowfin* (Fig. 1), a 114-foot, wooden-hulled ex-Army freight and supply ship, of the California Division of Fish and Game; the *Black Douglas* (Fig. 2), a 133-foot, steel-hulled ex-schooner, of the U. S. Fish and Wildlife Service; and two ex-Navy vessels, of the Scripps Institution (Fig. 3), the *Crest,* a wooden-hulled 136-foot minesweeper, and the *Horizon,* a steel-hulled, 143-foot tug.

Periodic cruises with three of these vessels are made throughout the year over an area extending from Oregon to central Lower California and to a distance of approximately 400 miles offshore. Each ship is at sea for a period of about two weeks in every month, occupying a series of 40–50 oceanographic stations (Fig. 4). At these stations, from observations of temperatures and salinities at 15 depths from the surface to 1,000 meters (Fig. 5), the course and velocity of the oceanic currents are estimated. Samples of water collected from each depth are analyzed for dissolved oxygen and phosphate content. Hauls with fine-meshed nets (Fig. 6) are made to determine the kinds, abundance, and distribution of small organisms, including fish eggs and larvae. Material is also collected for determination of the amount of microscopic plant life.

Previous Investigations

The Bureau of Marine Fisheries of the California Division of Fish and Game has been investigating the resource for nearly a third of a century. Within this period this agency has followed its growth from its beginning as a major fishery during the first world war, through its period of rather uniform expansion until 1936–37, through the years of seeming stability, to the recent epoch of reduced abundance. As a result, this is the better-documented fisheries in the worl

The changes in the sardine population b about by a rapidly increasing fishing pressu been observed since 1918. It was apparent ing the 1934–35 season that the catch pe of-effort was decreasing, even though th catch continued to rise and maintained level for ten years (Fig. 7). Despite im ments in vessels and gear, which greatly in the efficiency of exploitation, greater effo being expended to catch equivalent amou fish.

The California Division of Fish and Ga made many other important contributions to 1938 its scientists investigated sardine ing over much of its range off California an off Lower California, and established th area off southern California was an imp spawning center. In cooperation with ager British Columbia and in the states of Wash and Oregon, they conducted a tagging pr which showed that individuals move from so and central California to British Columb from the latter region to California. It wa cluded from these and other studies that the ies from British Columbia to southern Cal and even as far south as central Lower Cal were exploiting the same stocks of fish.

In 1938 the U. S. Fish and Wildlife Ser up the South Pacific Fishery Investigation headquarters at Stanford University, for th pose of augmenting research on this rapidly ing fishery. This group focused its attent the problem of age determination in sardin on the success of recruitment in relation to ographic conditions. Criteria were develo which the annual marks on scales and

FIG. 2. The *Black Douglas,* research vessel of t Pacific Fishery Investigations, U. S. Fish and Service, employed in recruitment and oceanogra search of the Cooperative Sardine Research

. The *Horizon,* left, and *Crest,* right, of the Scripps Institution of Oceanography, University of California,
n the oceanographic and recruitment studies of the Cooperative Sardine Research Program. The *Paolina*
has also been used in certain phases of the program.

cognized, and thus the age composition
tch determined rather accurately. The
the age composition of the commercial
n developed into a cooperative project
the U. S. Fish and Wildlife Service and
rnia Division of Fish and Game and is
carried on routinely, with the assistance
Columbia and the states of Washington
on. Undertaken as a cooperative program
Scripps Institution of Oceanography,
itment study foreshadowed on a modest
research that forms so important a part of
nt expanded program. Such cooperation
izes much of the Pacific sardine research.

Cause and Effect

f the fish in the commercial sardine catch
one to five years old. During the period
1, covered by routine age analysis, only
per cent of the fish have been six years
older. The age composition of the catch
rnia waters changes with the season, the
y taking mainly young fish and the average age increasing as the fishing season progresses. The average age of fish taken in the several fishing ports also increases from San Pedro to British Columbia. In the Pacific Northwest, fish have been available in quantity only during the summer months, whereas off California sardines are taken commercially from August through February. These facts have been interpreted as indicating that the fish move northward each summer and return in the fall and winter, the older fish reaching higher latitudes. The seasonal changes have not been as marked in recent years as formerly, mainly because the proportion of older fish in the population has been considerably reduced (Fig. 8). Before the recent decrease in landings, about 60 per cent of the catch in numbers was made up of fish three or more years of age, but since 1946 these ages have contributed only about 33 per cent of the total. In California waters fish of one or two years of age have become the chief support of the fishery, whereas in the Northwest the change in age composition in conjunction with a decline in abundance has led to the collapse of the fishery.

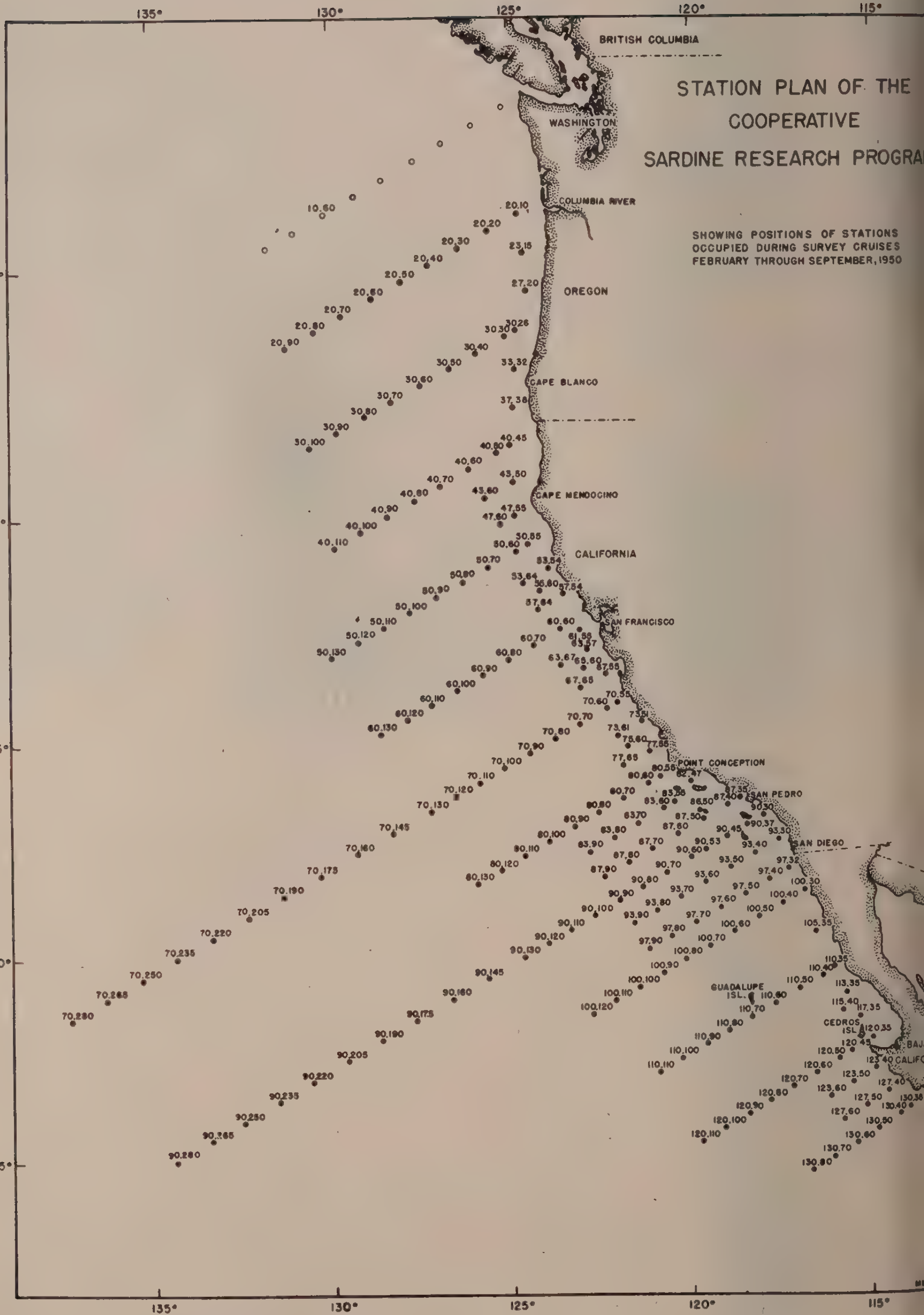
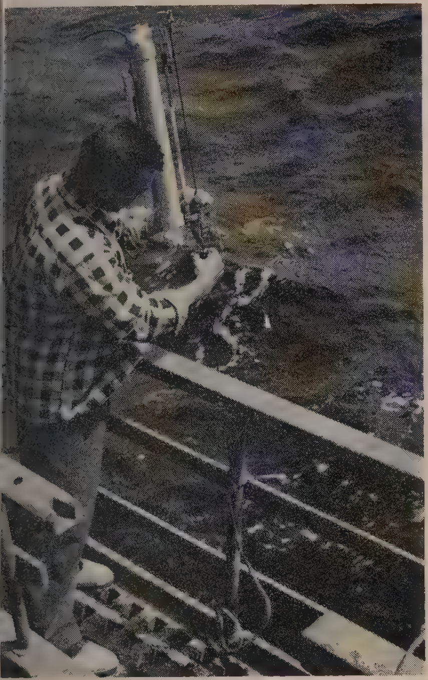

STATION PLAN OF THE
COOPERATIVE
SARDINE RESEARCH PROGRA
SHOWING POSITIONS OF STATIONS
OCCUPIED DURING SURVEY CRUISES
FEBRUARY THROUGH SEPTEMBER, 1950
BRITISH COLUMBIA
WASHINGTON
COLUMBIA RIVER
OREGON
CAPE BLANCO
CAPE MENDOCINO
CALIFORNIA
SAN FRANCISCO
POINT CONCEPTION
SAN PEDRO
SAN DIEGO
GUADALUPE ISL.
CEDROS ISL.
135°
130°
125°
120°
115°
45°
40°
35°
30°
25°

FIG. 4. Pattern of hydrographic stations off the west coast of North America. Most of the stations s
occupied at monthly intervals by the vessels of the Cooperative Sardine Research Program.



Jansen bottle attached to the wire preparatory
a hydrographic cast. A series of 15 such bottles
each station to measure temperature and to
er samples for determining salinity, oxygen,
nate content at appropriate depths from the
1,200 meters.

ted out previously, the Pacific coast sar-
ry has passed through three phases: a
ar period of rapid growth, a decade of
stant yield at a high level, and a sudden
ing decline amounting almost to collapse
ing ports except San Pedro. That the
on of 1936–37 was followed by a succes-
itful years of fishing was due largely to a
of good spawning seasons, climaxed by
of an unusually large year class spawned
Had it not been for these successful year
e collapse might have come much sooner.
other hand, continued spawning success
ve considerably delayed the collapse or
it entirely. In addition, the decline in
was accentuated by poor survival of the
, or by a change in availability.

haracteristic of pelagic-spawning species
e sardine that the survival of young from
s spawning varies greatly from year to
se that survive in a very favorable year
e many more times the number of fish to
ercial catch than do the recruits from a
r. During the early years of the fishery
iations in recruitment, although recognized by the biologists, were hardly obvious to the fishermen, because the fluctuations were hidden by the presence of relatively large stocks of older fish. Concurrently with increased fishing pressure—and in the opinion of many because of this pressure—this buffer was effectively reduced.

If the causes underlying the variations in survival of recruits from year to year can be detected, the success of each year class may be determined a year or two in advance of its entry into the fishery. The value of such information to the industry is recognized. The hope that such predictions could be made was a dominant factor in prompting the industry and the legislature to provide funds for expanding the research.

Objective of the Expanded Program

The main objective of the expanded sardine research program is to understand the sardine in relation to its physical and chemical environment, its food supply, its predators, and its competitors, and to evaluate such findings in terms of the survival of young and in terms of the distribution and availability of the sardines when they reach commercial size.

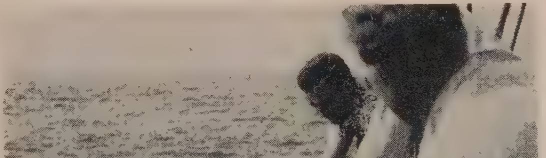


Fig. 6. Bringing the plankton net on board at completion of a haul. These nets, of fine-meshed silk, are provided with a meter in the mouth to measure the amount of water strained. They capture eggs and larvae of the sardine and of many other fish, in addition to providing a sample of the small organisms on which the sardine feeds.

Environmental relationships. Fluctuations in the sardine supply cannot be understood clearly without considering the interrelationships between the species and the physical, chemical, and biological conditions under which it lives. It is the task of the physical oceanographers in the program to provide data that will lead to a better understanding of the oceanic circulation off the Pacific coast of North America. Of particular importance is the necessity of measuring and recording seasonal and annual fluctuations in the horizontal and vertical circulation patterns. Both types of circulation may have significant effects on the distribution, survival, and availability of young and adult fish. The factors that control the vertical circulation are of particular interest in that they provide the mechanism by which the nutrient-rich subsurface waters, characterized by low temperature and high salinity, upwell into and fertilize the upper layers where plant growth takes place. Marine plants, the basic food producers of the sea, are confined to a surface layer seldom deeper than 300 feet, the depth of effective light penetration. The plants utilize certain essential chemical raw materials, such as nitrates and phosphates, that must be replenished constantly, or productivity will be low. It is now known that the duration and intensity of upwelling vary considerably from year to year and from place to place. An understanding of these variations may provide a clue to the distribution and success of year classes of sardines.

Survival and recruitment. Much of the research being conducted cooperatively by the Scripps Institution and the Fish and Wildlife Service is directed toward determining the causes underlying the success or failure of year broods of sardines. It is well established that survival varies considerably from year to year, for there appears to be no very consistent relation between the size of the spawning population and the number of recruits that it provides for the commercial fishery. The factors that effectively influence the survival of a year's brood of young are diverse and complicated. On hatching, the young sardine carries with it from the egg a supply of yolk that lasts only a few days. Before this food supply is exhausted, the tiny threadlike larvae, not much more than a sixth of an inch long, require, lest they perish, a supply of suitable food near at hand. This food must be small and must be present in quantity in the right place and at the right time, for the larvae have small mouths and are not active swimmers (Fig. 9). During the larval period they are subject to predation and competition from many sources, and perhaps also to epidemic disease. It it presumed that during these early stages the greatest mo occur.

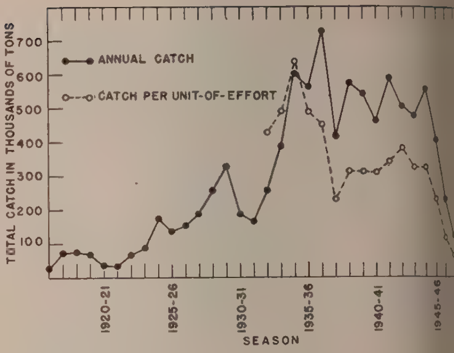


Fig. 7. Annual sardine landings in thousands for the entire Pacific coast, illustrating the early sion and recent decline of the fishery. The averag per unit-of-effort is shown from 1933 to date.

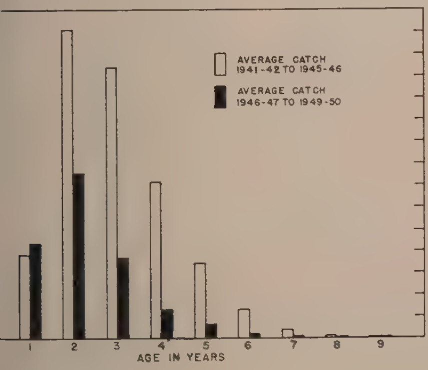
There is some evidence that the area of ing may vary considerably from year to ye that these annual variations have a bearing success of spawning. Although a large pro of the eggs are deposited in two major regi the coasts of southern California and central California, in certain years highly su spawnings may take place elsewhere. In th summer of 1939, for example, unusual n of nearly ripe sardines were taken in the off Washington, and in the spring and s of 1940 tremendous concentrations of you dines of the large 1939 year class were o in the waters of British Columbia and Wash It is possible that young of this year broo more abundant in the waters of the Pacific west than in the usual nursery grounds off ern and Lower California. The success 1939 year class may, therefore, have resulte an unusually wide distribution of spawnin der such conditions the chances for surv young fish should be greatly increased, for a greater bulk of food would be available o larger spawning area, and the chances wo greater that some groups of larvae wou counter particularly favorable conditions.

In order that the population be maintain constant level of abundance, only two resulting from the spawning of each femal survive to spawning age. A female sardine about 100,000 eggs per season, and her tot duction may amount to several hundred th eggs. Assuming that the number of eggs pr by a female during her life span is 200,000 a two fish resulting from her spawning reache mercial size, the resulting mortality from

be 99.999 per cent. If survival were
0 per cent, thus doubling the popula-
al mortality would be reduced by only
nt. In this connection it is possible that
raphic studies will provide informa-
ations in currents and in the physical
al properties of the ocean waters that
elated with the varying production of

lem of availability. Adult sardines are
ble to the fishery during some years
ers. This source of fluctuation in the
catch is being investigated by the
ivision of Fish and Game. The prob-
ally one of sardine distribution in rela-
sical, chemical, and biological oceano-
ditions. Schools located by echo-ranging
unding are sampled to determine the
-composition of the species present. In
eanographic observations are made and
auls taken for comparison with the
ntents of the fish. These observations
larger framework of the cooperative re-
a.

g the strength of year classes. The
a year class probably can be measured
ge following larval development, al-
with equal facility during the younger
e past a reliable measure has been pos-
fter the year class has entered the com-
hery. Since this method has limited
alue, it is important that estimates be
vance of recruitment into the commer-
The problem is being given considerable
the research program. Two methods of
the abundance of young sardines are
tigated. The first, employing quantita-
on-collecting procedures, will provide a
abundance and mortality during the early stages when the young fish are randomly distributed. The second, based on surveys on the nursery grounds, will provide an estimate of relative abundance of schooling young four to six months old. Several other lines of investigation may provide data for forecasting the strength of year classes. Physical and chemical observations may be found to fit patterns that vary in the same way as year-class strength. For example, there may be a direct correlation between intensity of upwelling and year-class strength, for which presumptive evidence has been found in the annual variation of salinities off the coast.



ge composition of the sardine catch before
e recent decline in sardine abundance.

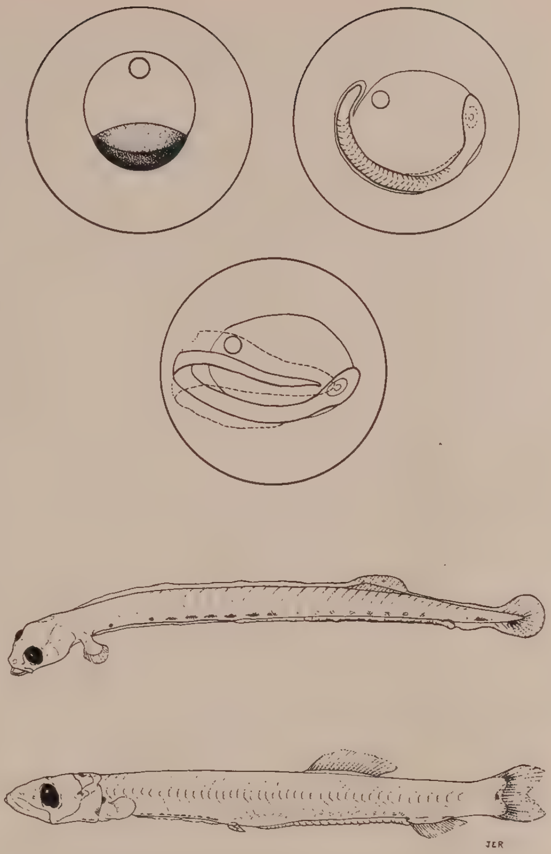


Fig. 9. Stages in the development of the egg and the larva of the Pacific sardine. The egg is approximately 1.7 millimeters in diameter. The two larval stages are about 10 and 25 millimeters long, respectively.

Recent Developments

Some important results have already been obtained. It has been confirmed that sardine spawning takes place in water of rather specific temperatures, almost entirely within the narrow limits 13°–16° C. The importance of the southern California region as a spawning area has been reemphasized, and further information has been gained on a second region of possibly even greater importance, lying to the south of Cedros Island off Lower California.

The surveys are yielding valuable information on the distribution, abundance, and life history of many species of fish. Much of this information should be of value to the sardine industry in indicating latent marine resources capable of being exploited in the lean years. Since there is a limit to the total amount of protein food that the ocean can produce, decrease in abundance of one species may be accompanied by proportional increases in others. If this be so, we cannot take full advantage of our fishery resource as long as we exploit only a part of it by concentrating on certain species. Consequently, the fuller utilization of such underexploited fishes as anchovy, saury, and jack mackerel should be encouraged. Major expansion of these fisheries should be accompanied by adequate biological studies. The information being gathered in the present surveys would be of considerable value in planning the research program and would contribute to the solution of the problems involved.

A development that will have far-reaching implications in oceanographic fisheries research has been made in the estimation of ocean currents. A method has recently been perfected by means of which the effect of rhythmic variations in density, apparently associated with tide-producing forces, may be eliminated from the determinations. Charts of current patterns, formerly characteri
complicated series of eddies, thereby hav
considerably simplified.

The requirements of the cooperative p
have stimulated the development of many r
improved types of oceanographic equipmen
standing is the high-speed plankton sample
vice that can be operated at top cruising spe
that gives a continuous record of both dep
the amount of water strained. To carry this
ment down and to maintain the desired d
especially designed bronze depressor is em
These and other developments have excit
siderable interest among scientists in many

The Pacific sardine is not disappearin
populations, whether exploited commerc
not, are subject to rather wide fluctua
abundance. The decline in sardine abu
seems to have been due to a succession
spawning seasons coincident with a chang
availability or an increase in the natural m
of adults. The European pilchard and the J
sardine fisheries have suffered similar dec
abundance. The catch of Pacific sardines
the current fishing season may reach 350,0
indicating that a substantial recovery is
place.

ILLUSTRATIONS: Fig. 1, Leo Pinkas; Fig. 2,
L. Wallis; Figs. 3, 5, and 6, John MacFall; F
and 8, drawn by Margaret Calderwood; Fig. 9,
Janet Roemhild.

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eprinted from Proc. zool. Soc. Lond. Vol. 121, Part II, pp. 515–527.]

egg and larval stages of *Nyctiphanes simplex*, a euphausiid crustacean from California.*

By

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[Communicated by Dr. E. Hindle, F.R.S.—Received January 25, 1951.]

(With 5 figures in the text.)

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Introduction.

n the coastal waters of California, particularly south of Point Conception, *tiphanes simplex* Hansen is frequently an extremely abundant form in the kton, ranking often second only to *Euphausia pacifica* Hansen as the erically dominant euphausiid. On account of their abundance, the larval es of these two species are doubtless of considerable importance in the eries and certainly play a large part in the general biology of the region. later larval stages of *E. pacifica* have been determined previously (Boden,)) and two of the furcilia stages of *N. simplex* have also been described nsen, 1912). However, no attempt has been made heretofore to describe he larval stages of *N. simplex.*

f the four species in the genus *Nyctiphanes* the larval stages of two have ady been described ; *N. couchii* (Bell) by Lebour (1924, 1925) and *N. australis* by Sars (1885) and Dakin and Colefax (1940). In spite of the thoroughness hese descriptions, reinvestigations are required on account of the work of donald (1927) and Fraser (1936), for nothing is known of the dominant es of these two species. The larval stages of the South African species *apensis* are still unknown.

This work was made possible by a grant from the Browne Research Fund of Royal Society, which is gratefully acknowledged. I should like to thank Marie Lebour and Mr. Ronald Keir, Marine Biological Association, and Martin Johnson, the Scripps Institution of Oceanography, for reading the uscript and for their stimulating criticism.

This study is contribution No. 509, New Series, from the Scripps Institution of nography.

Source of Material.

The material for this enquiry was drawn from the collections of the Marine Life Research Program of the Scripps Institution of Oceanography of the University of California. Ovigerous females and larvae were taken from the plankton and brought in formalin to this Laboratory for further examination. During this preliminary sorting the number of first stage furcilia obtained was, perhaps, insufficient to give a very clear indication of the dominant or typical form in this particular stage. However, the remaining dominant stages were clearly indicated on a frequency distribution (fig. 3), and no reasonable doubt can be entertained as to their identity, although the total number of furcilia examined (441) was somewhat smaller than could be desired.

Examination of a large number of plankton hauls taken from this region at all seasons of the year has shown that *Nyctiphanes simplex* (like *N. couchii* and *N. australis*) is typically a shallow-water neritic form. The larvae occur in all stages at all times of the year and the adults apparently spawn throughout the year. Ovigerous females appear in the plankton in appreciable numbers only in March and April, and between March and May there is a considerable increase in the numbers of *N. simplex* taken. That this increase is due largely to larvae is shown by the fact that in March, 1940, the ratio of adults to larvae taken in the nets was 3/1, while in May of the same year the same number of similar hauls yielded ratios of adults to larvae of 1/3. Thus, there appears to be greater spawning activity in the spring in this species, and in this it parallels the behaviour of the Atlantic form *N. couchii* (Lebour, 1924).

Development.

Egg.

The eggs are carried by the female in two pear-shaped sacs (fig. 1 A). These sacs are fixed along their anterior broad sides to the outer edges of the endopodites of the sixth and seventh cormopods, and by their narrow posterior ends to the exopodite of the eighth cormopod. The exopodites of the sixth and seventh cormopods are lacking in the female and that of the eighth cormopod is somewhat larger than in the male. There is a variable number of eggs in each sac; as many as thirty have been counted in each sac in some ovigerous females. The eggs measure 0·36–0·41 mm. in diameter, although they shrink somewhat in formalin. They are transparent and have an extremely small perivitelline space (fig. 1 B).

Nauplius stage.

As with other members of this genus, the naupliar stages of *N. simplex* are passed within the egg sac. A nauplius taken from the egg sac is shown in figs. 1 C, 1 D. The length range is from 0·40 mm. to 0·54 mm. The nauplius is simple and egg-shaped. Two small processes are visible at the posterior end of the carapace.

The first antennae project forward, are uniramous and unsegmented, and possess three short terminal setae.

The second antennae are antero-lateral and biramous, the rami with four and five setae respectively.

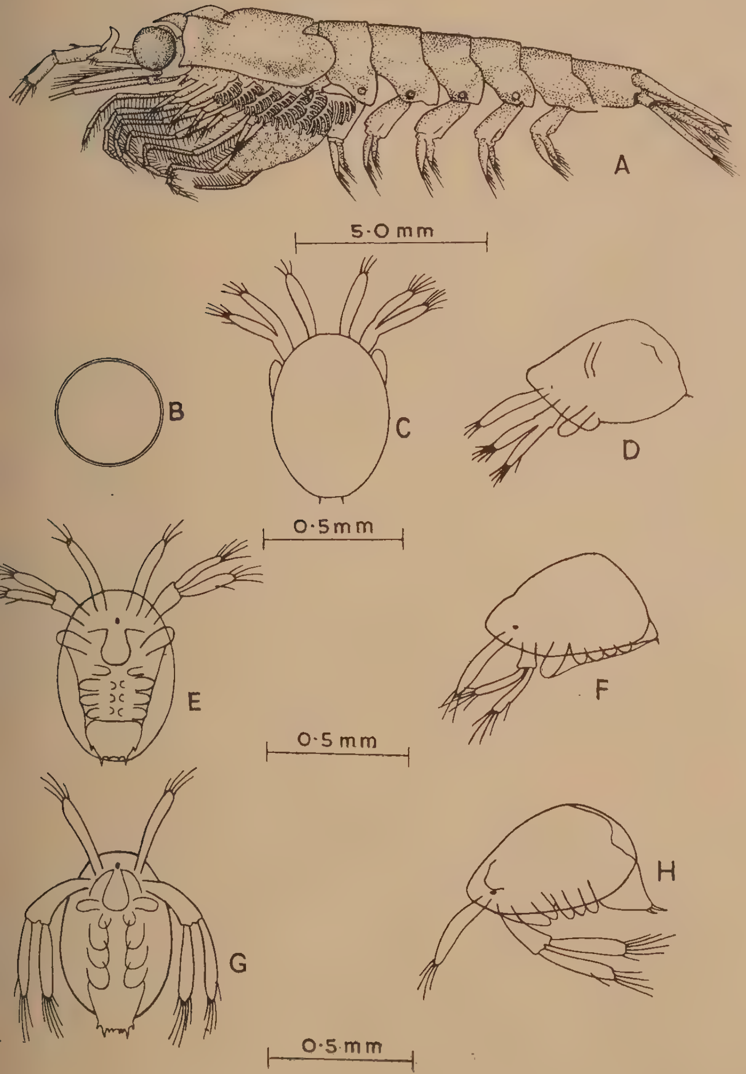
The mandible is uniramous and naked. This is the case in other members of the genus in which the naupliar stages are not free-swimming.

The nauplius gives rise to a pre-metanaupliar stage, known as the pseudo-metanauplius, while still in the egg sac.

Pseudo-metanauplius stage. (Figs. 1 E, 1 F.)

The larva probably emerges from the egg sac in this stage, but moults almost immediately into the next stage. This has been shown by rearing

Figure 1.



A. Ovigerous female, showing egg sac. B. Egg taken from sac.

Nauplius stage.

Dorsal view of specimen taken from egg sac. D. Lateral view of same specimen.

Pseudo-metanauplius stage.

E. Ventral view of specimen just hatched. F. Lateral view of same specimen.

Metanauplius stage.

G. Ventral view of metanauplius stage. H. Lateral view of same specimen.

experiments for *N. couchii* by Lebour (1924), and is substantiated by the fact that pseudo-metanauplii were seldom encountered in the plankton and only when ovigerous females were present. The pseudo-metanauplius has a length range of 0·54–0·60 mm. Viewed dorsally the carapace is oval.

The first antennae project forward, are simple and are armed terminally with three setae of moderate length.

The second antennae are biramous, each ramus having five setae.

The median eye is visible.

Rudiments of three metanaupliar limbs have appeared.

A short tail is held under the body and has one pair of postero-lateral spines and two pairs of terminal spines.

The carapace, uniramous mandibles, anterior lip, metanaupliar limb-buds and tail are all covered by an extremely thin skin.

Metanauplius stage. (Figs. 1 G, 1 H.)

The length range of this stage is 0·58–0·62 mm., which is a very slight increase in mean size over the preceding stage. The posterior part of the carapace is a little wider than the anterior.

The first antennae are unsegmented, uniramous and carry four terminal spines.

The peduncle of the second antenna projects laterally and the two rami sweep backward alongside the carapace. The rami bear five and six setae respectively.

The median eye is still visible and rudiments of the compound eyes have appeared.

The carapace, naked metanaupliar limbs and abdomen are now free. The abdomen projects downward and backward, tapers in lateral aspect and is armed with eight spines on its terminal margin.

The mandibles are reduced and bud-like.

The following three stages are the calyptopis stages, which are defined as the post-naupliar stages in which the carapace still completely protects the eyes.

First calyptopis stage. (Figs. 2 A, 2 B, 2 C.)

Length range : 0·99–1·31 mm. Average length : 1·02 mm.

The carapace covers the entire anterior part of the body and is without teeth or projections of any sort along its inferior margin. The length of the carapace is greater than half the length of the larva. The median eye is still present and visible, and on either side of it are the rudiments of the ocular luminous organs within the developing compound eyes.

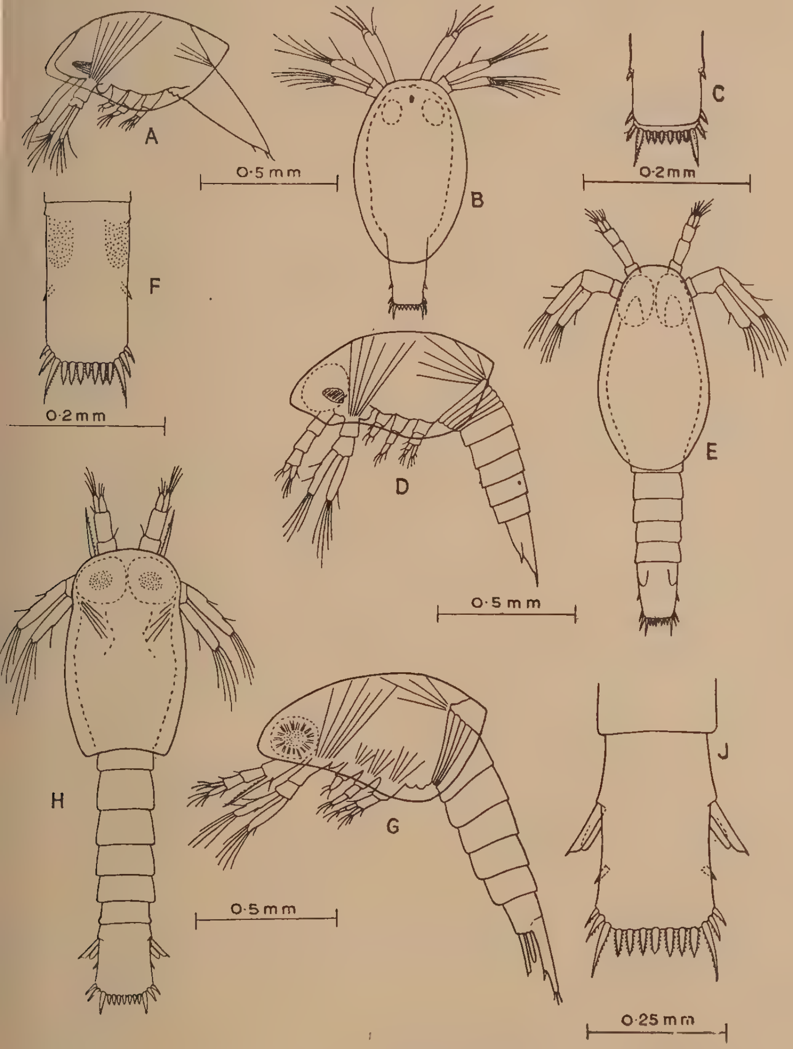
The first antennae are uniramous and project forward. Distally a small segment has developed, which carries three spines. At the outer distal end of the first segment are two spines of unequal length.

The peduncle of the second antenna has two segments. The first ramus of the second antenna is unsegmented and carries four terminal and two lateral spines. The second ramus is segmented at its distal end and carries six spines.

The first and second maxillae and first thoracic limb are present. These are all directed forward, are mobile and setose, and are used in feeding, this being the first stage in which the larva feeds actively. These appendages are figured for *N. australis* in greater detail by Sars (1885) and are essentially the same for this species.

The abdomen is unsegmented, but signs of later segmentation can be seen in the wrinkled integument of the anterior part. The terminal portion (later the telson) is provided with a pair of ventro-lateral spines, three pairs of postero-lateral spines and six terminal spines.

Figure 2.



First calyptopis stage.

A. Lateral view of whole animal. B. Dorsal view of same specimen.
C. Posterior end of abdomen showing ventro-lateral, postero-lateral and terminal spines.

Second calyptopis stage.

D. Lateral view of whole animal. E. Dorsal view of same specimen.
F. Telson from above showing rudiments of uropods within the integument.

Third calyptopis stage.

G. Lateral view of whole animal. H. Dorsal view of same specimen.
J. Telson from above showing developing uropods.

Second calyptopis stage. (Figs. 2 D, 2 E, 2 F.)

Length range : 1·35–1·75 mm. Average length : 1·50 mm.

The carapace is smooth along the inferior margin and is about half the total length of the larva. In *N. couchii* a lateral denticle develops in this stage (Lebour, 1924). This is absent in *N. australis* however, (Sars, 1885) as it is in this species. The median eye has disappeared and the compound eyes are now defined but not pigmented.

The peduncle of the first antenna has three segments and carries two rami distally. The outer of these rami carries five setae and the inner has three terminal setae.

The second antennae and remaining thoracic appendages remain as in the preceding stage but are somewhat larger.

Thoracic segmentation can be detected and the rudiments of the second cormopod are present.

The abdomen is divided into five segments and a telson. The uropods developing on the telson can be seen within the integument. The telson now has seven terminal spines in addition to the three pairs of postero-lateral spines and the one pair of ventro-lateral spines.

Third calyptopis stage. (Figs. 2 G, 2 H, 2 J.)

Length range : 1·80–2·26 mm. Average length : 1·95 mm.

The carapace is still without lateral denticles and is about half the total length of the larva. It completely covers the compound eyes, which are now clearly defined, globular and pigmented. Rudiments of the visual elements are discernible.

There are three segments to the first antennal peduncle ; the outer distal margin of the basal segment is produced as a strong, toothed spine which reaches beyond the distal end of the distal segment. The two rami of the first antenna are unaltered.

The second antenna, maxillae and first thoracic appendage remain unaltered but further development of the remaining thoracic limbs can be detected.

The musculature of the thorax is considerably advanced.

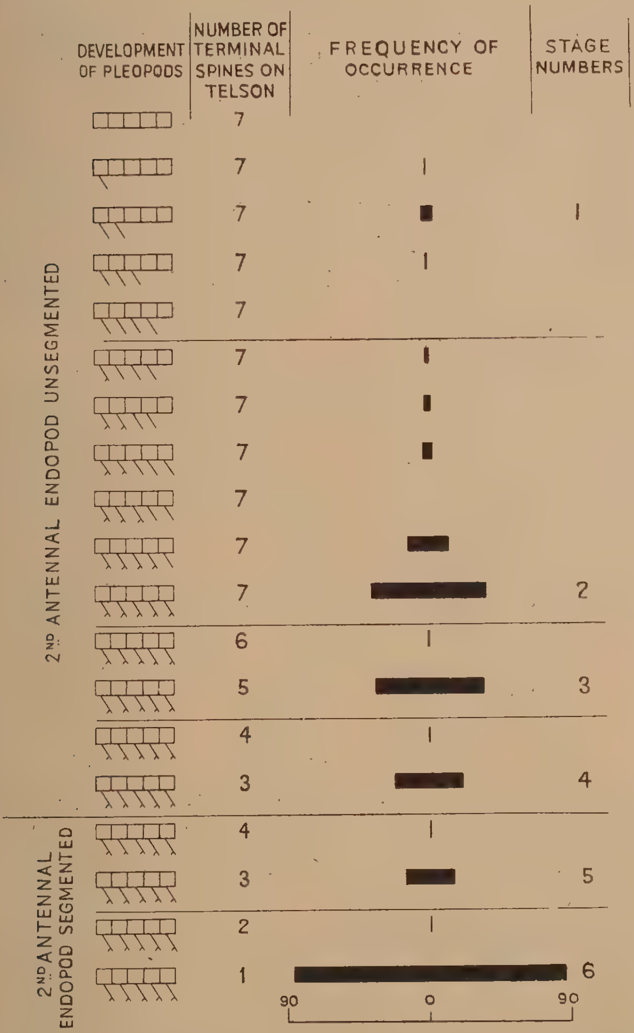
The abdomen now has six segments and a telson. There are as yet no traces of abdominal appendages. The uropods are biramous on a short basal segment ; the outer ramus is longer than the inner, and has its outer distal margin prolonged as a strong spine. The remaining armature of the telson is similar to that of the preceding stage.

Furcilia stages. (Figs. 3, 4.)

For reasons given before (Fraser, 1936 ; John, 1936 ; Einarsson, 1945 ; Boden, 1950), the term " calyptopis " for the earlier larval stages has been retained in this account, whereas the term " cyrtopia " for the later larval stages has been abandoned.

Gurney (1942, 1947) is in favour of retaining the term " cyrtopia " in order to emphasize the common ontogeny of all decapods. It is true that the change of shape of the second antenna which indicates the beginning of the " cyrtopia " is as important as the change of shape of the carapace which marks the beginning of the furcilia series or the change in the telson which marks the first juvenile. If the larva is to be characterized by function rather than form, the division between furcilia and " cyrtopia " is a natural one and should be retained. It is doubtful, however, whether the retention of the term " cyrtopia " does emphasize the phylogenetic relationships among the decapods. The terms " calyptopis ", " furcilia " and " cyrtopia " are peculiar to the Euphausiacea and, until a more uniform terminology has been devised for larval decapods in general, they emphasize little but divisions in the larval series of this particular order. The purpose of including the " cyrtopia ng the furcilia in this treatment is not so much to minimize the importance e division between the two, as to emphasize the continuity of a series in h dominant stages can be determined by statistical analysis. Gurney,

Figure 3.



grammatic key to furcilia stages and frequency of occurrence. The rectangles in the left-hand column represent the larval abdomen, each square being an abdominal segment. A simple stroke represents a non-setose pleopod; a feathered stroke represents a setose pleopod.

is comprehensive work on larval decapods (1942), tends to regard the rtopia " as post-larval and uses the terms " calyptopis " and " protozoea ", rcilia " and " zoea " as synonyms. However, there is usually evidence umping and dominance of certain of the " cyrtopia " stages, and on this

account they are regarded here as larval rather than post-larval and incluc
in the furcilia series, which is characterized by this phenomenon.

In the furcilia stages, therefore, are placed all larvae from those in wh
the carapace first withdraws from over the eyes and the telson is armed w
seven terminal spines and three pairs of postero-lateral spines, to those
which the telson has only one terminal spine but still retains three pairs
postero-lateral spines. After this the animal undergoes a number of regu
ecdyses until the adult form is reached. No dominant instars can be detec
at this stage which is considered “ juvenile ” or “ adolescent ”.

Sixteen types of furcilia larvae were encountered in the material examin
These were differentiated by variations in the development of the secc
antennal endopod and the pleopods, and by reduction in the number of termi
spines on the telson. It is suspected that three other types of furcilia may oc
occasionally, since they do in other species of this genus, but they were
found in this material. If they do occur it is probably rather infrequent
Six of these sixteen types were numerically dominant and are regarded
the six furcilia stages. Frequency distributions of these types are given
fig. 3.

The stages are as follows :—

FIRST FURCILIA. Pleopods non-setose. Second antennal endopod simple.

SECOND FURCILIA. Pleopods either mixed setose and non-setose or all setose. Sec
antennal endopod simple.

THIRD FURCILIA. All pleopods setose. Five terminal spines on telson. Second anten
endopod simple.

FOURTH FURCILIA. Three terminal spines on telson. Second antennal endopod simple.

FIFTH FURCILIA. Three terminal spines on telson. Second antennal endopod segment

SIXTH FURCILIA. One terminal spine on telson.

First furcilia stage. (Figs. 4 A, 4 B, 4 C, 4 D.)

The following furcilia types may be included in this stage :

(*a*) Those with no pleopods.
(*b*) ,, ,, one pair of non-setose pleopods.
(*c*) ,, ,, two ,, ,, ,, ,,
(*d*) ,, ,, three ,, ,, ,, ,,
(*e*) ,, ,, four ,, ,, ,, ,,
(*f*) ,, ,, five ,, ,, ,, ,,

Unfortunately, only eleven first stage furcilia were present in the mater
These belonged to (*b*), (*c*), and (*d*) as follows : (*b*)—2, (*c*)—7, (*d*)—2. Stage (
is taken as being represented by (*c*), therefore, although this may be a m
representation due to the small number of larvae examined. It is suspec
that (*f*) does not occur in this species, nor in any other species of the gen
since it has never been described. It is almost certain, however, t
representatives of (*a*) and (*e*) have been missed. The form with two pa
of non-setose pleopods has been illustrated in figs. 4 A, 4 B, 4 C, 4 D.

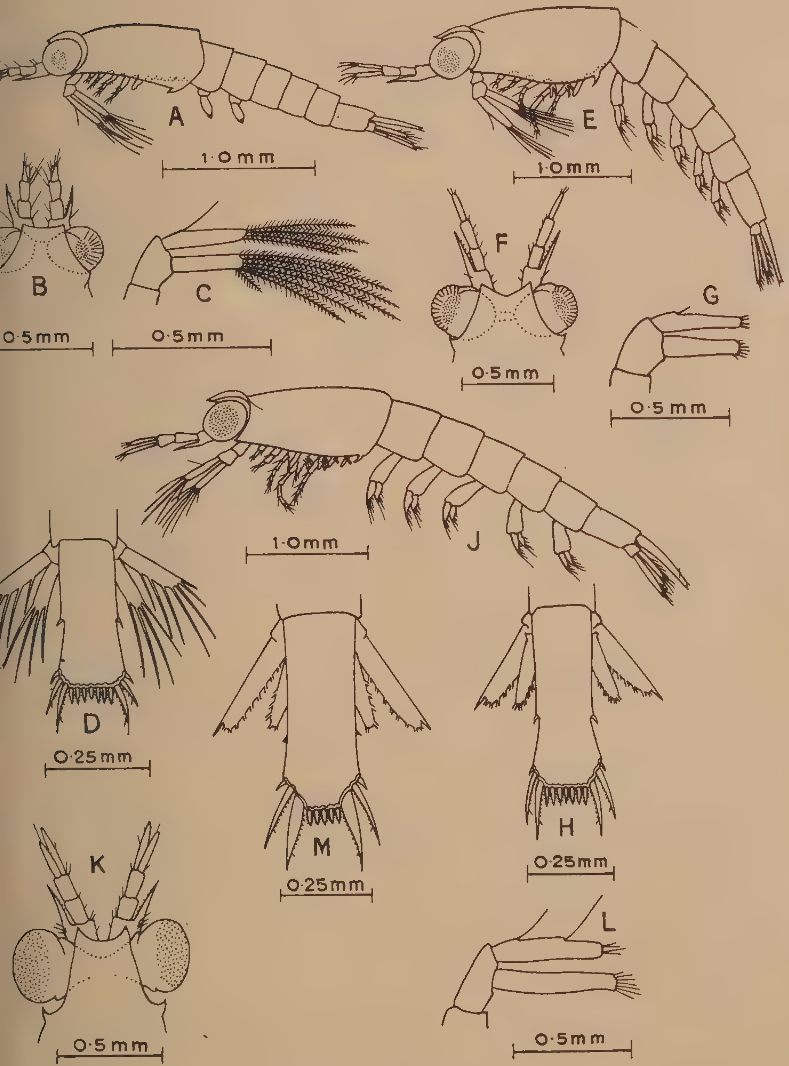
The length range is 2·4–2·9 mm. with an average length of 2·6 mm.

There are no rostral processes on the carapace. The frontal plate
broader than long, with a flat to concave anterior margin. Posteriorly
carapace is rounded and it has a small denticle on the inferior margin.
eyes project beyond the edge of the carapace and are darkly pigmented.

The peduncle of the first antenna has three segments, of which the ba
bears a strong spine on the outer margin. This does not quite extend to
distal end of the terminal segment.

The second antenna is biramous and natatory. Its endopod is unsegment
The first two cormopods are segmented and the third is present as a roun
lobe.

Figure 4.


A
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J
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D
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M
0·25 mm
H
0·25 mm
K
0·5 mm
L
0·5 mm

First furcilia stage.

A. Lateral view of whole animal. B. Dorsal view of anterior part of body. C. Second antennal endopod. D. Telson and lateral uropods from above.

Second furcilia stage.

Lateral view of whole animal. F. Dorsal view of anterior part of body. G. Second antennal endopod. H. Dorsal view of telson and uropods.

Third furcilia stage.

Lateral view of whole animal. K. Dorsal view of anterior part of body. L. Second antennal endopoed. M. Telson and uropods from above.

The telson is considerably elongated and the uropods well developed. Ther are seven terminal spines, three pairs of postero-lateral and one pair of ventr lateral spines.

Second furcilia stage. (Figs. 4 E, 4 F, 4 G, 4 H.)

In this stage the larva has either mixed setose and non-setose pleopods o all setose pleopods. Included are the following types :

(*a*) Those with 4 pairs of pleopods : 1 setose, 3 non-setose.
(*b*) ,, ,, 4 ,, ,, ,, 2 ,, 2 ,,
(*c*) ,, ,, 5 ,, ,, ,, 2 ,, 3 ,,
(*d*) ,, ,, 5 ,, ,, ,, 3 ,, 2 ,,
(*e*) ,, ,, 5 ,, ,, ,, 4 ,, 1 ,,
(*f*) ,, ,, 5 ,, ,, ,, all setose ; the terminal spines on the telson remai unchanged.

All these forms were present in the material except (*d*). This form, wit three setose and two non-setose pleopods, undoubtedly does occur, bu probably in very small numbers. Corresponding stages have been reporte for *N. couchii* (Lebour, 1925), and for *N. australis* (Dakin and Colefax, 1940) In all, 112 larvae belonging to the second furcilia stage were examined an these were distributed as follows : (*a*)—3, (*b*)—5, (*c*)—7, (*d*)—0, (*e*)—25 (*f*)—72. The frequency distribution for these types in *E. pacifica* was bimoda and a separation was evident between the forms with mixed setose an non-setose pleopods and those with all setose pleopods. There is no evidenc of such a separation in *N. simplex* and these types are all placed in the secon furcilia stage. The possibility exists that the form with four pairs of setos and one pair of non-setose pleopods is an extra stage. This could be ascertaine by direct observation on moulting specimens.

The length range for this stage is 3·3–4·5 mm. ; for form (*f*) it is 4·1–4·5 mm with an average length of 4·3 mm.

The frontal plate of the carapace is similar to that in the preceding stage or perhaps a little more emarginate. The lateral denticle on the posterior en of the inferior margin of the carapace is very pronounced.

The flagella of the first antenna are elongate but still unsegmented. Th peduncle is unchanged.

The second antenna remains unchanged with the endopod still simple.

The second cormopod is long, the third is already segmented and the fourt is present as a rounded lobe. The first gill-lobes can be distinguished on th second and third cormopods.

The five pairs of pleopods have all developed, are biramous and setose.

The telson still has seven terminal spines.

Third furcilia stage. (Figs. 4 I, 4 J, 4 K, 4 L.)

This stage contains larvae in which the number of terminal spines on th telson has been reduced to five. All pleopods are setose and the endopod o the second antenna is simple. Sixty-eight specimens belonging to this stag were found in the material. Also encountered in the collection were two larva with six terminal spines on the telson. These have not been included in any particular stage since they are regarded as abnormalities (Fraser, 1936 John, 1936).

The length range in this stage is 4·2–4·6 mm. and the average length is 4·3 mm.

The carapace remains unaltered, except the frontal plate, which has elongated. The eyes are now heavily pigmented.

The peduncle of the first antenna is essentially similar. However, the segments have elongated so that the strong spine at the distal end of the basal segment now reaches just beyond the distal end of the second ıent. The flagella are also longer than in the preceding stage, being now ›st as long as the peduncle.

The second antenna remains unaltered.

There are now five cormopods, the first to the third with their segmentation plete, and the fourth and fifth unsegmented. Gill-lobes are present on fourth and fifth.

The telson is armed with one pair of ventro-lateral, three pairs of postero-ral and five terminal spines. The innermost pair of the postero-lateral es has changed shape and the bases are now considerably wider (about quarter as wide as they are long).

rth furcilia stage. (Figs. 5 A, 5 B, 5C, 5D.)

The endopod of the second antenna is still simple at this stage, but the ıinal spines of the telson are only three in number. Forty-one specimens nging to this stage were present in the material examined. Also present, not assigned to any particular stage, were two larvae with four terminal es on the telson.

The length range is 4·5–4·8 mm. and the average length is 4·6 mm.

There is no change in the carapace or eyes.

The first antennal flagella are as long as the peduncle, and the spine on distal outer margin of the peduncle is now very strong and pronounced, icularly at its base.

The second antenna has not altered.

There are now seven cormopods. The fifth, sixth and seventh are still mentary. The fourth is fully segmented but lacks an exopodite.

The telson carries one pair of ventro-lateral, three pairs of postero-lateral three terminal spines.

h furcilia stage. (Figs. 5 E, 5 F, 5 G, 5 H.)

In the earlier terminology this would constitute the first cyrtopia stage. re was a total of thirty larvae in this stage, with a length range of -5·3 mm. The average length was 4·9 mm.

The frontal margin of the frontal plate is no longer markedly concave but early straight.

The flagella of the first antenna are segmented and longer than the peduncle. upper distal margin of the basal segment of the peduncle shows the ıments of the lappet which is characteristic of the adult.

The outermost segment of the second antennal peduncle bears a spine on outer distal margin. The exopod of the second antenna is now a scale, ing setae, while the endopod is non-setose and divided into three segments.

The seven cormopods of the adult are all present, the sixth with only four nents and the seventh still unsegmented. The first signs of sexual orphism are apparent in this stage for the female lacks the exopodite of sixth cormopod, whereas it is present in the male.

The telson carries three terminal spines and is the same as in the preceding e.

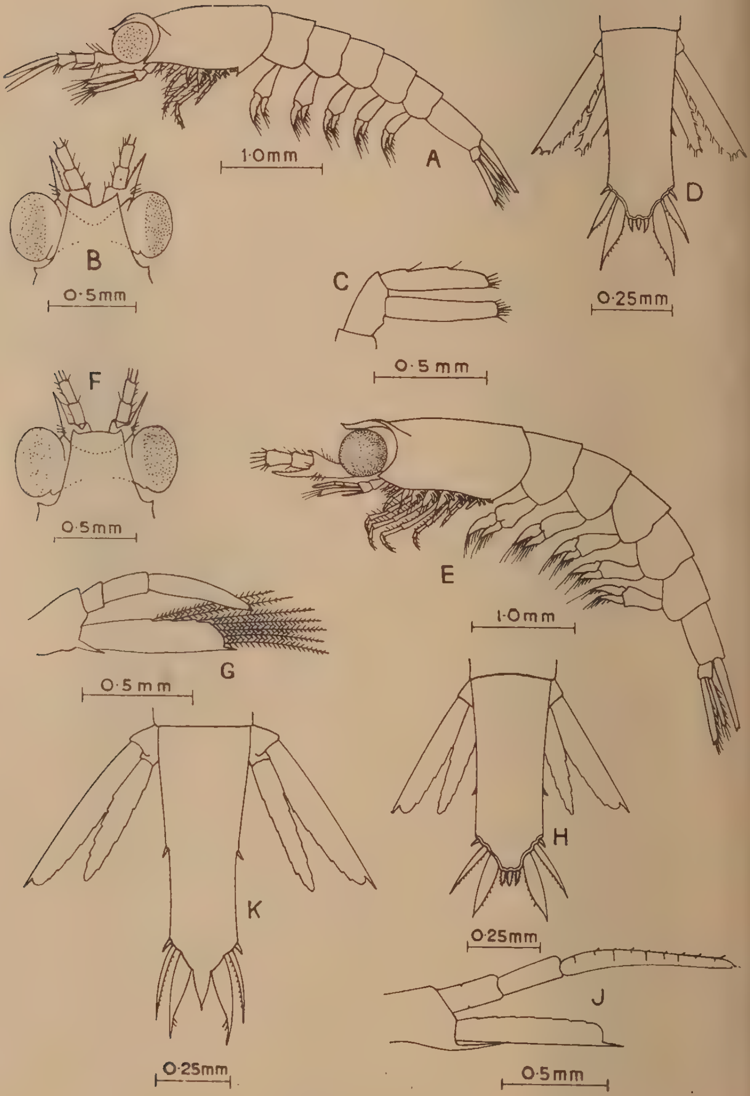
h furcilia stage. (Figs 5 J, 5 K.)

The final furcilia stage is essentially similar in appearance to the previous and, therefore, has not been figured completely. This stage was esented by 172 larvae. Twenty-five of these were measured and gave a th range of 5·1–6·0 mm. with an average length of 5·6 mm.

The rostrum is a little shorter than in the previous stage and the tooth on inferior margin of the carapace has disappeared.

The endopod of the second antenna is just over half as long again as the pod. It now bears setae and shows the beginning of further segmentation. exopod now carries setae along the entire length of its inner margin.

Figure 5.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H
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J
0·25mm
0·5mm

Fourth furcilia stage.

A. Lateral view of whole animal. B. Dorsal view of anterior art of body.
C. Second antennal endopod. D. Dorsal view of telson and lateral uropods.

Fifth furcilia stage.

E. Lateral view of whole animal. F. Dorsal view of anterior part of body.
G. Second antennal endopod showing segmentation. H. Telson and uropods from abo

Sixth furcilia stage.

J. Second antennal endopod. K, Dorsal view of telson and uropods, The telson now bears only one terminal spine, but retains three pairs of tero-lateral spines. The wide inner pair of these have only two teeth on ir inner margin. In *N. couchii* (Lebour, 1925) these disappear completely, l the outer long laterals lose their teeth, too, before they themselves are arded. *N. simplex* appears to retain the teeth along the inner margins of outer laterals as long as it retains the laterals.

eniles.

The juvenile differs diagnostically from the final furcilia stage in having y two pairs of postero-lateral spines on the telson, the outer long laterals ring been discarded.

Individual variation makes it difficult to assign a definite number of instars the species between the final furcilia and the adult. On the whole, the mal appears to undergo about nine or ten ecdyses in the juvenile condition. se are rather orderly, each instar being a little more complicated than the , and there is no evidence of dominance of any of the stages. Having ched adult form (the animal may be sexually mature before this), *N. simplex* tinues to grow, sometimes attaining lengths between 16 and 17 mm.

Summary.

The female of *Nyctiphanes simplex* carries her eggs in an egg sac. The eggs ch in the nauplius stage and remain in the egg sac throughout that stage. larva emerges from the sac as a pseudo-metanauplius and moults nediately into the metanauplius stage. This is followed by three calyptopis ges and the furcilia stages. There are probably nineteen types of furcilia rae. Since six of these are numerically dominant, it is probable that the rae "jump" stages in the furcilia series. The six dominant types are cribed as the six furcilia stages. A key to the furcilia stages is included.

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BULLETIN OF THE GEOLOGICAL SOCIETY OF AMERICA
VOL. 62, PP. 707-724, 1 FIG., 2 PLS. — JULY 1951

ARITE CONCRETIONS FROM THE OCEAN FLOOR

By Roger Revelle and K. O. Emery

Abstract

dging from the sea floor off California recovered about 6 kilograms of tubular, sub-spheri-
gular shaped barite concretions embedded in marine mud. These are poorly sorted in weight
ange from 1 to 25 centimeters in length. The physical, chemical, and mineralogical charac-
odules are described and compared with those of other barite concretions found on land or
e sea floor. Barium sulphate is present in amounts up to 77 per cent, in the form of small
s often within the tests of Pliocene Foraminifera.

es of the origin of barite concretions are discussed and tested in terms of those character-
to be of genetic importance. It is believed that the most probable mode of origin was the
erstitial sulphate-rich sea water of the sediment with ascending magmatic waters contain-
rium and strontium. Various bits of evidence suggest that the two other reported occur-
concretions on the sea floor had a similar origin.

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Introduction

3, a program of geological inves-
e ocean floor off the California
coast was carried on under the direction of Dr. F. P. Shepard, as a project of the Geological Society of America. In the course of this work, a series of dredgings was made from the

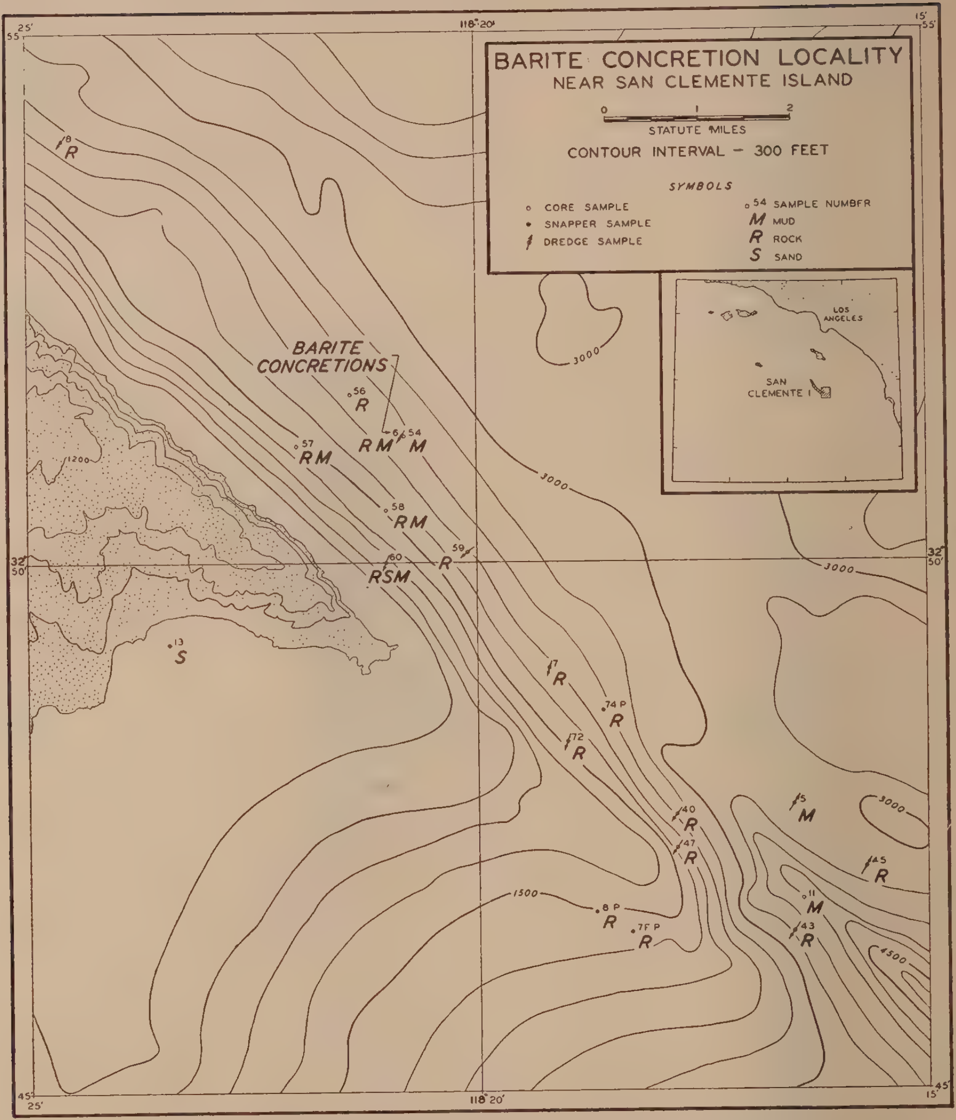

BARITE CONCRETION LOCALITY
NEAR SAN CLEMENTE ISLAND
0 1 2
STATUTE MILES
CONTOUR INTERVAL – 300 FEET
SYMBOLS
CORE SAMPLE
SNAPPER SAMPLE
DREDGE SAMPLE
54 SAMPLE NUMBER
M MUD
R ROCK
S SAND
LOS ANGELES
SAN CLEMENTE I
BARITE CONCRETIONS
118°20'
25'
55'
15'
32°50'
45'
8 R
56 R
57 RM
6 54 RM M
58 RM
59 R
60 RSM
13 S
7 R
74 P R
72 R
40 R
47 R
8 P R
7F P R
5 M
45 R
11 M
43 R
1200
1500
3000
4500

FIGURE 1.—BOTTOM TOPOGRAPHY OFF SAN CLEMENTE ISLAND
Showing position of Station 6 where a dredging recovered barite concretions. Note locations of adjacent samples in which the concretions were absent.

vessel E. W. SCRIPPS along the probable fault scarp which forms the north-east side of San Clemente Island (Fig. 1). One of these, made at a depth of 800 to 650 meters, recovered about 100 kilograms of green mud which contained 250 loosely mixed concretions. A few angular fragments of andesite were also present. The area of occurrence of the concretions is apparently very limited because none were found in later dredgings and cores from the same vicinity.

ACKNOWLEDGMENTS

The discovery of the concretions was made possible by a grant of the Geological Society of

America which permitted the taking of a large number of sea floor dredgings off California, one of which encountered the barite locality. Especial gratitude is expressed to Mr. M. L. Natland, who identified the Foraminifera within the concretions and the mud matrix. Appreciation is also due to Dr. F. P. Shepard and to Dr. R. S. Dietz, both of whom offered many helpful suggestions during the investigation. Assistance in the preparation of these materials was furnished by the personnel of Works Projects Administration, Official Projects 165-03-6999 and 465-03-3-403.

Table 1.—Weights and Average Bulk Specific Gravity of Different Types of Concretions

Type of concretion	Number	Average weight grams	Range in weight grams	Per cent of total weight	Average bulk specific gravity	Range in specific gravity
Tubular warty	7	15	5–61	2.1	3.27	3.20–3.36
Rounded warty	4	96	25–244	7.6	2.73	2.62–2.78
Flat warty	59	12	5–63	13.4	2.72	2.52–2.93
Tubular smooth	27	49	10–180	25.9	2.70	2.20–3.18
Irregular warty	12	98	15–920	23.2	2.67	2.43–3.08
Rounded smooth	49	29	4–256	27.8	2.62	2.31–2.93
Median		60			2.69	
Enclosing mud					1.51	1.42–1.69
Moreno nodules	20				3.67	3.20–3.88

General Characteristics

The concretions range from less than 1 cm. to about 25 cm. long, and in weight from about 2 grams to nearly 1300 grams, with a median weight of 60 grams. They are poorly sorted; the weight distribution curve has maxima in the weight groups of 10–20, 80–160, and 640–1280 grams. The latter fraction, however, contains only one concretion. The total weight of all concretions is 6 kilograms.

The nodules were classified according to shape as: (1) tubular, elongate, or ellipsoidal, (2) equidimensional, or subspherical, (3) thin and flat, and (4) irregular or branching. Some of the concretions have warty or rough surfaces, occasionally with nipple-like protuberences. The remainder are relatively smooth (Pl. 1). In general, the smooth ones are softer and more friable than those with rough surfaces.

In contrast to the greenish-gray mud in which they occur, the concretions with rough surfaces are brownish-gray, while the smooth ones are similar in color to the mud. Many concretions of various types have a relatively hard and compact outer shell surrounding a softer core of more porous appearance (Pl. 2, fig. 1). The outer shell may consist of several layers, and is generally darker than the core.

An approximate measure of the bulk specific gravity of many of the concretions was obtained after they had been washed free of the enclosing mud and dried. The weight was determined with a spring balance, and the volume by measuring the amount of water that they displaced. No relation between size and bulk specific gravity was observed (Table 1). With one exception, the rough-surfaced concretions have higher average bulk specific gravities and a smaller range in bulk specific gravity than the smooth ones. Table 1 also shows for comparison the bulk specific gravity of the mud in which the concretions were found and of a group of barite nodules from the Cretaceous Moreno shale, near Coalinga, (Anderson and Pack, 1915) kindly sent to us by Dr. Ralph Stewart, of the U. S. Geological Survey. The sea floor concretions are considerably denser than the surrounding mud, but much less dense than the Moreno shale concretions. It will be shown later that this difference is due to a lack of pore space in the Cretaceous concretions.

A pipette mechanical analysis of the enclosing mud gave a median diameter of 4 microns and a sorting coefficient of 5.5. The sample contained 11 per cent sand, 36 per cent silt, 22 per cent clay, and 31 per cent colloid.

Petrographic Examination

Examined in thin-section, the concretions are found to consist in part of barite and in part of clay, detrital minerals, and organic remains. The barite occurs chiefly as small radial aggregates that range up to 0.2 mm. in diameter. These are commonly closely interlocking but the interference crosses of individual aggregates are easily observed by revolving the microscope stage under crossed nicols (Pl. 2, fig. 2). Barite is present in larger, more definite aggregates in the outer layer of a zoned concretion than in the core. Most of the aggregates include clay grains and some even contain a large detrital grain. Barite crystals are best developed inside the tests of Foraminifera. Because of the small size of the crystals, the indices of refraction could not be measured accurately, but were observed to lie between 1.63 and 1.65.

Beside barite and clay grains, the inorganic constitutents include plagioclase (chiefly labradorite), basalt-andesite fragments, glauconite, and minor amounts of augite, hornblende, biotite, collophane, and hematite. Siliceous sponge spicules, calcareous echinoid spines, and foraminiferal tests are also present. The general absence of quartz and the arkosic nature of the sand grains reflects the basic character of the rocks of San Clemente Island from which the detrital material may have been derived.

In the concretions of tubular, rounded, or irregular shape, fine-grained materials predominate, and minerals other than barite and clay never exceed 10 per cent. The flat concretions contain a much larger proportion of coarse grains, chiefly plagioclase, glauconite, and foraminiferal tests (Pl. 2, fig. 3).

Spectrographic Examination

A concretion of the round smooth type, the separated outer and inner portions of one of the tubular smooth group, and a sample of the enclosing mud were examined spectrographically by Dr. T. G. Kennard (Table 2).

Barium is present in relatively large quantities in the concretions but is found only as a trace in the mud. Likewise, strontium is more abundant in the concretions. All of the other major constituents except potassium appear to be present in approximately equal amounts in the concretions and the mud. Nickel and fluorine are more abundant in the mud, while lead and titanium are less abundant or absent.

A comparison of the spectrographic results with the very complete chemical analysis of a composite sample of green and blue muds published by Clarke (1924) shows certain qualitative differences in the content of minor elements. Boron, gallium, fluorine, and lithium were found only in our material, while vanadium, arsenic, molybdenum, and zinc, although listed by Clarke, were not detected in our samples.

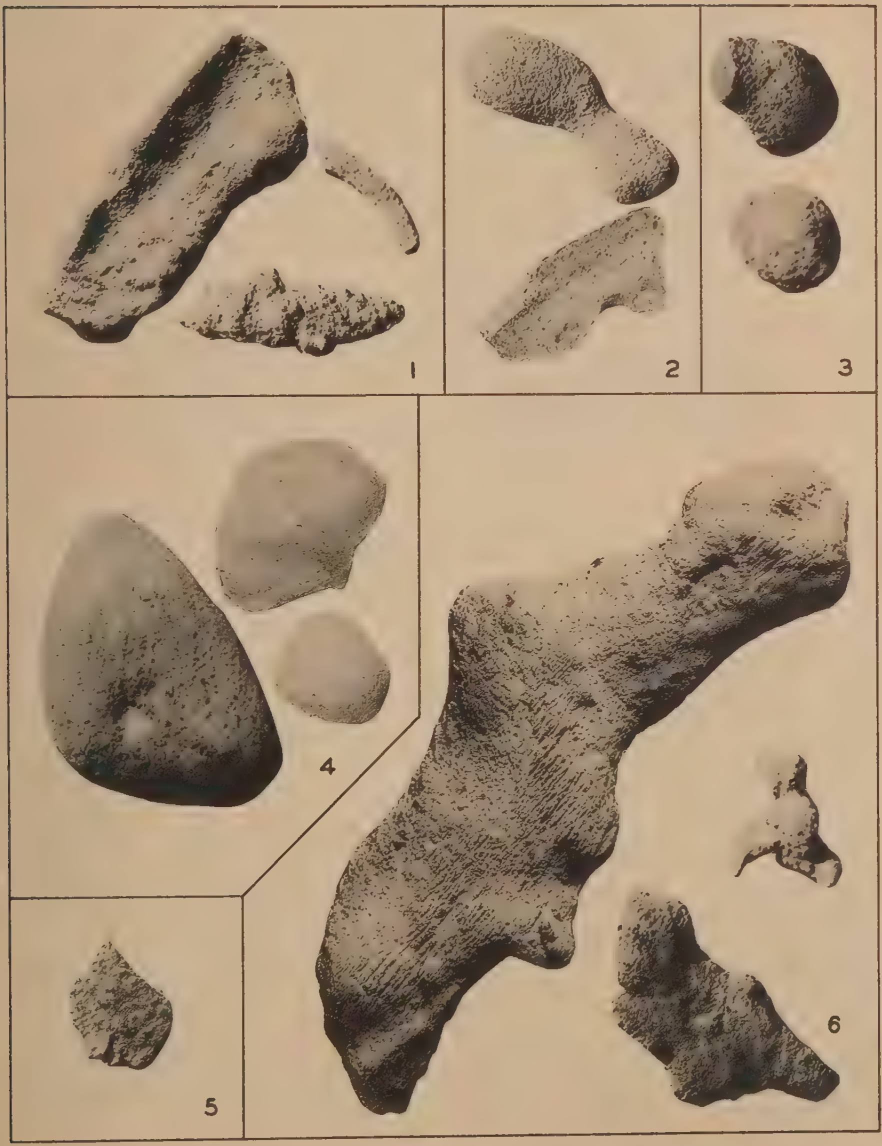
Chemical Analyses

Methods

The samples that were examined spectrographically were also chemically analyzed, principally by Mr. J. D. Laudermilk. Air-dried samples weighing approximately half a gram were used. After determination of ignition loss, the material was treated with boiling 10 N. hydrochloric acid and the acid-soluble and insoluble fractions were then analyzed separately. Barium was obtained by dissolving a portion of the acid-insoluble fraction with hot concentrated sulphuric acid, filtering and precipitating as the sulphate. Silica remaining in the precipitate was removed by evaporation with hydrofluoric acid.

Plate 1.—SHAPES AND SURFACE CHARACTERS OF CONCRETIONS

Showing the six groups described in the test: (1) tubular warty; (2) tubular smooth; (3) round warty (4) round smooth; (5) flat warty; and (6) irregular warty. Scratches on large one were produced by brushing. × 0.4



SHAPES AND SURFACE CHARACTERISTICS OF CONCRETIONS

FIGURE 1

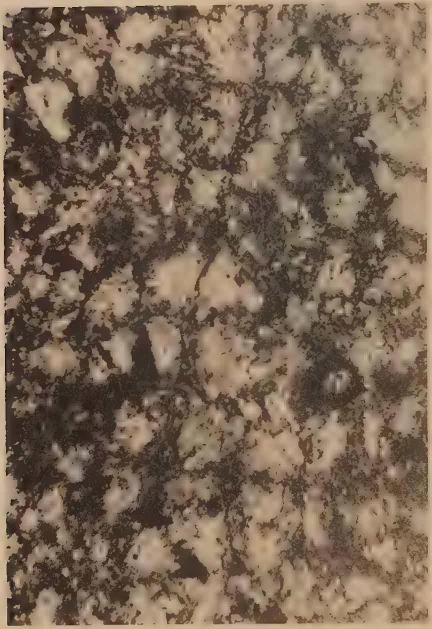


FIGURE 2

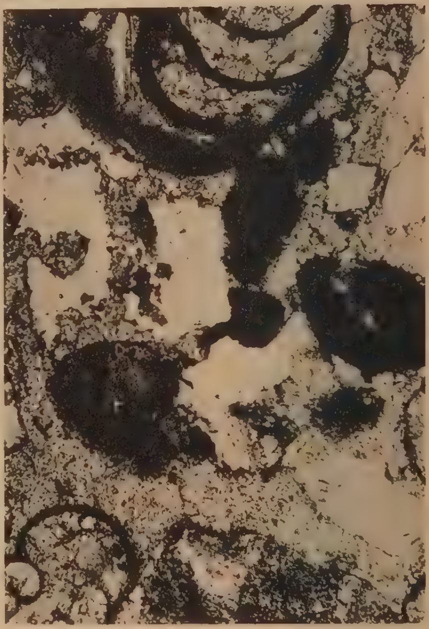


FIGURE 3

SECTIONS OF CONCRETIONS

The remainder of the acid-insoluble fraction was fused with sodium carbonate. Analyses of silica, iron (as the sesquioxide), calcium, and magnesium in this fusion and in the acid-soluble fraction were carried out by standard methods (Hillibrand and Lundell, 1929). Sulphate was precipitated as $BaSO_4$ from the water soluble part of the sodium carbonate fusion. Strontium was not determined separately, but was probably precipitated in large part with the calcium. In a separate investigation, Mr. Howard T. Odum found that the ratio of strontium to calcium atoms in another one of the concretions was 0.070. If this ratio is correct for the concretions of Table 3, SrO would constitute 0.49, 0.47, and 0.93 per cent, respectively with CaO reduced in proportion.

Separate samples had to be taken for the determination of P_2O_5, Al_2O_3, and F because of interference between these substances. The P_2O_5 was determined in the usual manner by means of ammonium molybdate in nitric acid solution, after three evaporations to dryness to eliminate chlorine. In the Al_2O_3 determination, fluorine, which prevents complete precipitation of alumina by ammonia, was first removed by evaporation to fuming with sulphuric acid. Fluorine was determined by a quantitative spectrographic method. Sodium and potassium were determined directly on a separate portion, after a fusion with ammonium chloride and calcium carbonate, as uranyl zinc sodium acetate and potassium cobaltinitrate, respectively. Water was determined separately only on the mud, using a modified Penfield method. The percentage of CO_2 was estimated from the amount of acid-soluble calcium. Dissolved chloride was measured by titration of the solution obtained from repeated leaching of the samples with distilled water. In Table 3, it is assumed for simplicity that the chloride is present exclusively as NaCl.

TABLE 2.—SPECTROGRAPHIC EXAMINATION OF BARITE CONCRETIONS AND ENCLOSING MUD*

	Tubular Smooth Concretion		Round Smooth Concretion	Enclosing Mud
	inside	outside		
Al	X	X	X	X
B	0.0X	0.0X	0.0X	0.0X
Ba	XX	XX	XX	0.0X
Ca	XX	XX	XX	XX
Cr	0.0X	0.0X	0.0X	0.0X
Cu	0.0X	0.0X	0.0X	0.0X
F	—	—	—	X
Fe	X	X	X	X
Ga	0.0X	0.0X	0.0X	0.0X
K	0.X	0.X	0.X	X
Li	0.0X	0.0X	0.0X	0.0X
Mg	X	X	X	X
Mn	0.0X	0.0X	0.0X	0.0X
Na	X	X	X	X
Ni	—	—	—	0.0X
Pb	0.0X	—	—	—
Si	X	X	X	X
Sr	X	X	X	0.X
Ti	0.X	0.X	0.0X	0.0X

* Examination by Dr. T. G. Kennard. Tests were also made with negative results for the following elements: Ag, Au, As, Be, Bi, Cb, Cd, Ce, Co, Cs, Ge, Hf, Hg, In, Ir, La, Mo, Os, Pd, Pt, Rb, Re, Rh, Ru, Sa, Sb, Sc, Sn, Ta, Th, Tl, V, W, Y, Zn, Zr.

Explanation of Symbols:
XX = large amount >10 per cent
X = moderate amount 10–1 per cent
0.X = small amount 1–0.1 per cent
0.0X = traces only <0.1 per cent
— = none found

Results

Barite content.—Barium sulphate in the analyzed concretions varies from 62 to 77 per cent (Table 3). Bjerrum's analysis of nodules collected by the SIBOGA expedition in the

PLATE 2.—SECTIONS OF CONCRETIONS

FIGURE 1.—POLISHED SECTION SHOWING CONCENTRIC ZONING IN THE TUBULAR SMOOTH CONCRETION SELECTED FOR CHEMICAL ANALYSES

Note the alternating light and dark bands in the outer shell. × 15

FIGURE 2.—THIN-SECTION UNDER CROSSED NICOLS OF CONCRETION SHOWN IN FIGURE 1

Note interference crosses of barite spherulites. × 100

FIGURE 3.—THIN-SECTION OF FLAT WARTY CONCRETION UNDER PLANE POLARIZED LIGHT

Dark-gray portions are calcite (note foraminiferal tests); white areas are plagioclase or holes in section; large black spots are glauconite; light-gray groundmass is barite. × 30

East Indies (Bøggild, 1916) gave 82 per cent $BaSO_4$. Jones (1887) guessed that the nodules from the sea bottom near Ceylon contained about 75 per cent $BaSO_4$. An analysis by Chukhrov (1937) of concretions from the Pliocene of the Kertch Peninsula shows 82 per cent $BaSO_4$. According to analyses by Nichols (1906) and Shead (1923), the sand barites of Oklahoma contain from 52 to 55 per cent $BaSO_4$. The concretions from the Cretaceous Moreno shale, previously mentioned, appear to have from 40 to 65 per cent $BaSO_4$, the higher percentage being from the pisolitic crust. The outside shell of the tubular smooth concretion analyzed by us also contains a higher percentage of $BaSO_4$ than the core.

Comparisons of concretions and mud matrix.—No barium was detected by chemical means in the mud matrix of the concretions. On the other hand, appreciable amounts of fluorine and phosphate were found only in the mud. These may be combined with calcium in the form of the mineral collophane. When a comparison of the concretions and the mud is made on a barite-free basis, several other differences are evident. The amounts of iron and alumina are much higher in the concretions than in the mud,

TABLE 3.—CHEMICAL ANALYSES OF BARITE CONCRETIONS

	Oklahoma Sand Barites		Kertch Nodules Chukhrov[3]	Kai Island Nodules Bøggild[4]	California sea floor concretions			
	Nichols[1]	Shead[2]			Tubular smooth		Round smooth	Mud matrix
					(Inside)	(Outside)		
SiO_2	36.99%	45.13%	9.41%	6.42%	9.87%	6.95%	10.81%	23.18%
Al_2O_3	5.36	0.88	5.56	2.32	3.99	3.76	4.39	7.16
Fe_2O_3	0.82	0.96	1.06	1.67	2.35	2.26	3.67	
MgO	0.03	0.00	0.65	0.42	0.97	0.48	0.98	1.80
CaO	0.51	0.00		2.01	4.40	4.21	8.38	29.40
BaO	35.76	34.25	53.22	53.85	47.92	50.96	40.91	0.00
Na_2O[5]					n. d.	n. d.	0.28	2.62
K_2O					n. d.	n. d.	1.66	0.58
SO_3	19.20	17.87	28.12	28.56	25.02[6]	26.42	21.33[6]	n. d.
P_2O_5			0.25		tr.	tr.	tr.	0.62
NaCl[7]					n. d.	n. d.	.76	2.21
F					n. d.	n. d.	n. d.	0.42[8]
CO_2[9]					0.86	1.78	5.77	22.03
H_2O	0.27	0.31	1.39	2.94	3.99[10]	2.97[10]	1.86[10]	3.49
Org. m.	0.32	0.00	n. d.					4.56
MnO		0.02	0.20					
TiO_2			tr.					
Total	99.26%	99.42%	99.86%	98.19%	99.28%	99.79%	100.80%	98.07%
$BaSO_4$[11]	54.41%	52.12%	81.88%	81.85%	72.94%	77.54%	62.24%	0.00%

1. See Nichols (1906).
2. See Shead (1923)
3. See Chukhrov (1937).
4. See Bøggild (1916).
5. Computed from total Na—Na required to balance Cl.
6. SO_3 computed from % BaO.
7. Computed from dissolved chloride determination.
8. Determined spectrographically.
9. CO_2 computed from acid soluble CaO.
10. Organic matter plus water equal loss on ignition minus computed CO_2.
11. $BaSO_4$ computed from % BaO.

whereas calcium carbonate is higher in the mud than in any of the concretions analyzed.

A considerable part of the calcium and strontium of the concretions was acid-insoluble and therefore could not have been present as a carbonate. It is possible that this acid-insoluble material was chiefly strontium sulphate. This possibility is supported by the results of an attempt to determine the amount of soluble sulphate in the concretions and in the enclosing mud using the conductimetric titration method of Anderson and Revelle (1947). Barium chloride was added to suspensions of the mud and of a powdered concretion and the end point was determined by a sharp increase in conductivity. The apparent amount of soluble sulphate relative to dissolved chloride was about twice as great in the concretion as in the mud. This would be true if $SrSO_4$, which is more soluble than $BaSO_4$, were present in the concretions. The barium added during the titration would not only precipitate with the dissolved sulphate ion but would also replace strontium in $SrSO_4$.

Even after allowance is made for sodium balanced against chloride, there are considerably greater amounts of sodium in the mud than in the one concretion in which alkalies were determined. Potassium, on the other hand, is more abundant in the concretion than in the mud. This reversal of the sodium-potassium ratios may indicate a replacement of the exchangeable sodium of the concretions with other cations.

Specific Gravity and Porosity

One to six gram fragments of different types of nodules were dried overnight at 105°C and weighed. Their volumes were determined by weighing the mercury that was displaced when the nodules were immersed in a mercury-filled pyknometer. The ratio of weight to volume was taken as the bulk specific gravity of the fragments. After being crushed, the samples were placed in a pyknometer filled with petroleum ether of determined specific gravity. The grain specific-gravity was taken as the ratio of the weight of the pulverized fragments to the volume of ether displaced. Duplicate determinations were made by the same procedure using kerosene as the immersion liquid.

Bulk specific gravities of the samples vary between 2.43 and 3.01, while the grain specific gravities range from 3.44 to 3.97. For comparison, pure barite averages 4.35. In contrast, the bulk specific gravity of the mud is only 1.13 and the grain specific gravity is 2.51. The measured grain specific gravities agree fairly closely with those computed from the chemical analyses (Table 4). The percentage of pore space, calculated from the difference between the bulk and grain specific gravities, is also shown in Table 4.

Table 4.—Specific Gravity and Porosity of Individual Concretions

Type of Concretion	Bulk Specific Gravity	Grain Specific Gravity	Calculated Grain sp. gr.	Porosity
Tubular warty	2.88	3.97		27.5%
Tubular smooth, outer shell	3.00	3.88	3.90	22.7
Tubular smooth, core	2.77	3.64	3.82	23.9
Tubular smooth	2.74	3.44		20.3
Round smooth	3.01	3.71		18.9
Round smooth	2.43	3.66	3.63	33.6
Flat warty, shelly	2.44	3.54		31.1
Irregular warty, partly shelly	2.99	3.47		13.8
Average	2.78	3.64		23.6
Enclosing med	1.13	2.51		54.9

Porosity is rather variable and high, ranging from 13.8 to 33.6 per cent and averaging 24 per cent. The average barium sulphate content computed from the specific gravities is 62 per cent by weight, or 50 per cent by volume. The volume occupied by barite plus the pore space equals 74 per cent, a value perhaps the same as the original porosity. While the actual measured porosity of the enclosing mud was only 55 per cent, a porosity of 74 per cent, which implies a water content of 52 per cent by wet weight, is well within the range of recent marine muds. The Moreno shale concretions, unlike those from the sea bottom, apparently have little or no remaining pore space, because their bulk specific gravity corresponds with the density computed from a rough chemical analysis.

By comparing the water contents of the

TABLE 5.—FORAMINIFERA IN CONCRETIONS AND ENCLOSING MUD*

Species	Age	Relative Abundance	
		Concretions	Mud
Angulogerina occidentalis (Cushman)			C
Angulogerina semitrigona (Galloway and Wissler)		C	
Bolivina acuminata Natland			R
Bolivina advena var. *striatella* Cushman			RC
Bolivina cf. *pisciformis* Galloway and Morrey	XXX	R	RC
Bolivina seminuda Cushman			RR
Bolivina sinuata Galloway and Wissler	XXX	R	RR
Bolivina spissa Cushman	X	R	A
Bolivina sp.	XXX		R
Bolivinita angelina (Church)	XX	C	
Bolivinita sp.	XXX		A
Bulimina cf. *affinis* d'Orbigny			C
Bulimina cf. *fossa* Cushman			R
Bulimina cf. *inflata* Sequenza	XX	C	A
Bulimina pagoda Cushman			R
Bulimina spinifera Cushman			RC
Bulimina subacuminata Stewart and Stewart			RC
Cassidulina californica Cushman and Hughes		C	
Cassidulina delicata Cushman	X	C	C
Cassidulina laevigata d'Orbigny			RC
Cassidulina lomitensis Galloway and Wissler		C	
Cassidulina quadrata Cushman and Hughes		A	A
Cassidulina tortuosa Cushman and Hughes		VA	
Cassidulina translucens Cushman and Hughes	XX	R	
Cassidulina tumida Natland			R
Cassidulina sp.	XXX	C	
Chilostomella ovoidea Reuss			RR
Cibicides cf. *basiloba* (Cushman)	XXX	C	R
Cibicides cf. *fletcheri* Galloway and Wissler		A	R
Cibicides mckannai Galloway and Wissler	XX	A	A
Cibicides repettoensis LeRoy	XX	VR	
Cibicides spiralis Natland	XX	R	
Discorbis rosaceus (d'Orbigny)		R	R
Ehrenbergina bradyi Cushman	X	VR	
Epistomina elegans (d'Orbigny)	X	VR	
Eponides frigidus (Cushman)		R	
Eponides subternera (Galloway and Wissler)			R
Eponides umbonata (Reuss)	XX	R	RR
Frondicularia advena Cushman			R
Glandulina laevigata d'Orbigny			R
Globigerina bulloides d'Orbigny		A	VA
Globigerina conglomerata Schwager			A
Globigerina inflata d'Oribgny			R
Globigerina quinqueloba Natland			VA
Globigerinoides minuta Natland			C
Globorotalia scitula (Brady)			C
Globorotalia truncatulinoides (d'Orbigny)			VR
Gyroidina soldanii var. *altiformis* Stewart and Stewart	XX	C	C
Lagena elongata (Ehrenberg)			R
Laticarinina pauperata (Parker and Jones)			R
Martinottiella communis (d'Orbigny)			R

TABLE 5.—FORAMINIFERA IN CONCRETIONS AND ENCLOSING MUD (*Continued*)

Species	Age	Relative Abundance	
		Concretions	Mud
Nodogenerina advena Cushman and Laiming	XXX		RR
Nodogenerina lepidula (Schwager)	XX	C	A
Nodosaria arundinea Schwager	XXX	R	C
Nodosaria hispida d'Orbigny		VR	
Nodosaria subsoluta Cushman	XX	R	
Nodosaria tosta Schwager	XXX	R	C
Nodosaria sp.	XXX		R
Nodosaria sp.	XXX		RC
Nonion pompiloides (Fichtel and Moll)	XX	A	VA
Nonion umbilicatula var. *pacifica* (Cushman)	X	R	A
Nonionella turgida (Williamson)			R
Orbulina universa d'Orbigny		C	A
Planulina aff. *ariminensis* d'Orbigny	XX		R
Planulina ornata (d'Orbigny)		C	A
Plectofrondicularia californica Cushman and Stewart	XXX	C	R
Pleurostomella sp.	XXX		R
Polymorphina charlottensis Cushman		R	
Polymorphina lactea (Walker and Jacob)			VR
Pseudoparrella pacifica (Cushman)	X	R	
Pullenia bulloides (d'Orbigny)	XX	R	RC
Pullenia salisburyi R. E. and K. C. Stewart		R	
Pyrgo serrata Bailey			RC
Sigmoilina tenuis (Czjzek)			C
Sphaerodina bulloides d'Orbigny			RR
Textularia flintii Cushman			R
Uvigerina ampullacea H. B. Brady			RC
Uvigerina canariensis d'Orbigny			R
Uvigerina peregrina Cushman	X	R	A
Uvigerina peregrina var.			A
Uvigerina senticosa Cushman	XX	VR	A
Uvigerina sp.	XXX	VR	R
Valvulineria araucana (d'Orbigny)	XX	VR	RC
Valvulineria inequalis (d'Orbigny)			R
Virgulina nodosa R. E. and K. C. Stewart			R
Virgulina schreibersiana Czjzek			R

* Age:
X Known from Pliocene and only rarely in Recent sediments as shallow as the dredging.
XX Known from Pliocene but not Recent sediments as shallow as the dredging.
XXX Extinct and not present in rocks younger than Middle Pico, Pliocene.

Abundance: VA, very abundant; A, abundant; C, common; RC, rather common; RR, rather rare; R, rare; VR, very rare.

mud and of a concretion as calculated from the porosity with the total weight of chloride determined by chemical analysis, we find that the chlorinity of the interstitial water of the concretion is 33 parts per thousand, and the chlorinity in the mud is 27 parts per thousand. These values contrast with the usual chlorinity found in muds off the California coast, 19 parts per thousand.

FORAMINIFERA

Several specimens of the concretions and of the enclosing mud were examined for foraminiferal content by Mr. M. L. Natland, of the Richfield Oil Company. He distinguished 86 different species or varieties (Table 5). Of these, 26 were found in both concretions and mud, 17 in concretions alone, and 43 in mud alone.

Foraminifera of the mud were much easier to separate and study than those enclosed in the barite concretions, thus probably accounting for the large number of species found only in the mud.

According to Natland (1933), eight out of forty-three, or 19 per cent of all the species found in the concretions are now extinct and are not present in rocks younger than Middle Pico age (Upper Pliocene). Fourteen species, or 33 per cent definitely are not found in recent sediments at depths as shallow as that of the dredging in which the concretions were found, but do occur in Pliocene sediments. Seven other species, or 16 per cent are also present in the Lower Pliocene and only rarely occur this relatively shallow depth in recent sediments. Although the remaining 32 per cent of the species are found in recent sediments at the depth of the dredging, they are also present in Lower Pliocene sedimentary rocks. The Foraminifera of the enclosing mud have an age distribution essentially similar to that of the concretions.

From the foraminiferal evidence it is thus possible to conclude that the concretions were either formed in Pliocene sediments or in younger sediments consisting very largely of redeposited Pliocene materials. Formation of the nodules might have occurred during or after Repetto time (Lower Pliocene).

Occurrences of Barite in Sediments

Concretions from the Recent Sea Floor

Only two other occurrences of barite concretions in recent sediments dredged from the sea floor have been reported in the literature. This may reflect a real scarcity of such nodules, or it may be due to the small area of the ocean bottom represented in dredgings. The most widely known find is that made by the British surveying ship, Investigator, in 1235 meters off Colombo, Ceylon. According to Jones (1887), the nodules collected by the Investigator are irregularly rounded, varying in shape from almost spherical to roughly cylindrical. They range in size from 2 to 10 centimeters. The surfaces are said to be rough with small pits and protuberences. Barite is present as small radial aggregates, with glauconite and remains of Foraminifera and Radiolaria sparsely scattered throughout the concretions. Some of the shells of Foraminifera and Radiolaria enclose spherulites of barite. On the basis of a rough partial chemical analysis, Jones estimated that the nodules contain 75 per cent $BaSO_4$, together with small quantities of strontium and other elements. The specific gravity was determined as 3.77. No barium was detected by qualitative analysis of the mud that enclosed the nodules.

On the Dutch Siboga expedition to the East Indies in 1899 and 1900, barite concretions were dredged in blue mud from a depth of 304 meters near the Kai Islands. These concretions (Bøggild, 1916), have a maximum diameter of 6 centimeters. They are brownish-gray and are flat or irregular in shape with smooth surfaces. Some are compact; others are loose and porous. Many are hollow with an inside crust, or a geode-like lining of small barite crystals. The texture is fine-grained. Clay minerals, iron oxide, free silica or opal, and calcium carbonate of foraminiferal tests accompany the barite, which is present in amounts up to 82 per cent. The sample in which the barite nodules were found also contained concretions of iron sulphide.

From the descriptions and illustrations given by Jones and Bøggild, it is apparent that the concretions examined by them are similar in nearly every respect to those from the California sea floor. The nodules from off Colombo may be classed with our round smooth and tubular types, while those from off the Kai Islands belong to the irregular and flat groups.

Fossil Occurrences of Nodular Concretions

Occurrences of nodular barite concretions of various degrees of purity have been described by numerous authors from sedimentary rocks that range in age from Early Permian to Pliocene (Twenhofel, 1932).

Barite concretions of rounded, elliptical, or irregular form occurring in the Lower Permian of southwestern Oklahoma were mentioned by Tarr (1933) in a comprehensive discussion of barite rosettes from that state. These range from 1 to 8 centimeters in diameter and have either pitted or rough sandy surfaces. The concretions with pitted surfaces consist of pure barite, occurring in a complicated structure of dominantly radial fibres, whereas those with rough sandy surfaces are massive and seem to be the result of cementation of sandstone. No suggestion as to the origin of the barite or the mode of precipitation was given.

From the Triassic of Bidston Hill, England, Moore (1898) described globular sand concretions the size of walnuts, which contain up to 34 per cent barite. Mackie (1901) cited the widespread occurrence of arenaceous barite nodules having as much as 37 per cent $BaSO_4$ scattered through the Triassic sandstone along the coast of Elginshire. Globular barite concretions with pitted and crenulated surfaces from the Upper Lias of France were mentioned by Collot (1905), who reported that previous authors had described them as remains of sponges and polyps.

The earliest reference to barite concretions of which we are aware is the mention by Georgi in 1798 of "Schwerspathbälle am Ufer der Sura und Piana" in the Jurassic of northeastern European Russia. These were later described by Samoilov (1917) together with other occurrences in Upper Jurassic and Cretaceous marine clays of a very large area. The barite appears in various forms, sometimes as nodules of characteristic shapes, elsewhere as a filling in marly septaria, and occasionally in phosphatic concretions. The widespread nature of the occurrences, all of the same geologic age, suggested to Samoilov that the barite had been deposited on the sea floor by a particular group of organisms which had flourished during later Jurassic time, and that the concretions had resulted from subsequent diagenetic concentration. Previously, Schulze (1905) and Thierfelder had shown that granules of $BaSO_4$ occur in the bodies of Xenophyophora, a group of marine rhizopods. These organisms are mostly confined to low latitudes, but range widely in depth, from 1 or 2 meters in coral reefs to more than 4000 meters. Samoilov thought that the observed presence of Xenophyophores in the ocean near Ceylon might be related to the finding in the same locality of the barite concretions described by Jones, and Andrée (1920) assigned the origin of the concretions collected by the SIBOGA Expedition to the activity of these organisms.

Rounded and slightly flattened sand barite nodules of Cretaceous age from the Libyan Desert were mentioned by Zittel in 1883. Pogue (1911) discussed the occurrence in the same general area of a few concretions of mammillary structure mixed with numerous barite rosettes. From California, barite nodules were reported by Anderson and Pack (1915), embedded in the Upper Cretaceous Moreno shale near Coalinga. Some characteristics of these nodules have already been mentioned.

Eocene concretions from the Yazoo clay of Louisiana were described by Hanna (1936). These have diameters up to 10 or 12 cm. and are composed of aggregates of pisolites consisting of nearly pure barite. The centers are commonly hollow with groups of irregular cavities which are free of foreign material. No mode of origin was suggested. In the Sahara Desert the Nubian sandstone, also Eocene, contains barite rosettes (Walther, 1912).

Delkeskamp (1900) published an extensive report on the marine Tertiary baritic sandstones of the Wetterau and Rheinhessen districts of Germany. Both rosettes and concretionary forms containing up to 80 per cent barite occur in the sandstones. Many of the concretions are spherical and possess a radial structure; others are irregular, with vegetable-like forms. Reis (1921) and Geib (1937) described the Middle Oligocene barite concretions from Steinhart in the Rheinhessen District, which were among those mentioned by Delkeskamp. These commonly have nuclei of molluscan shells or plant remains. Delkeskamp thought that ascending hot solutions containing barium had been forced to spread out through the sandstone because of the presence of an overlying impermeable layer of clay. Reis and Geib also assigned the origin of the barium to hot springs, but thought that the concretions were formed while the sediments were being deposited. According to Geib, the sulphate necessary for the precipitation of barium resulted from the decomposition of the soft parts of the molluscs whose shells were enclosed by the concretions. Several objections to this hypothesis are apparent. The most important is that the dissolved sulphate in the interstitial sea water of the marine sand would have sufficed to precipitate the barium.

Large concretions in Miocene marl of the

Lower Alps were mentioned by Collot (1905) who states that they are made up of radial aggregates of barite crystals.

Rounded, cylindrical, and irregular-shaped concretions containing up to 81 per cent barite from the Pliocene sedimentary iron ores of the Kertch Peninsula in Russia were analyzed and described by Chukhrov (1937). These nodules have a dense or finely crystalline structure, with veinlets of a lighter color and inclusions of öolitic iron ore, quartz, and clay. The surfaces are rough or mammillary. Chukhrov considered that the barite was originally present as a colloidal precipitate from which larger crystals later developed. As characteristic features of such metacolloidal barite, he lists: (1) rounded nodules having more or less smooth or tubercular surfaces, commonly with dehydration cracks; (2) cryptocrystalline texture, resulting in dense and earthy aggregates; (3) öolitic, pisolitic, concretionary, or septarian shapes; (4) mechanical admixtures and inclusions of materials other than barite; and (5) fibrous, radially arranged crystals formed principally from comparatively pure colloidal suspensions.

Other Types of Sedimentary Barite

Besides occurring as nodular or irregular concretions, barite is present in many other forms in sedimentary rocks. Perhaps the most spectacular are the barite rosettes and dollars, described by numerous authors including Tarr (1933) from the Lower Permian of Oklahoma; Pogue (1911) from the Cretaceous of Egypt; and Richardson (1923) from the English Lias. Veins and larger crystals of barite in lime concretions were mentioned by Martens (1925); similar occurrences in Paleozoic limestone and red beds were discussed by Dickson (1902) and Howland (1936). Barite cementing Triassic and other sandstones of England and elsewhere has been reported (Clowes, 1899; Greenwood, 1920), and barite crystals in pyritized ammonite shells were mentioned by Collot (1905). All of these authors believed that the barium had been carried to a point of deposition by percolating ground water which had previously encountered and leached barium-containing minerals or rocks. Little consideration was given to the mechanism of precipitation, except by Dickson and Tarr, who thought that the formation of barite occurred when the percolating ground waters containing barium ion mingled with other waters containing sulphate or came in contact with either gypsum or pyrite, which furnished the necessary sulphate.

Barite deposits in pipes carrying water from certain British coal mines were reported by Clowes (1889). Öolites and pisolites of barite apparently formed in oil wells by precipitation from brines have been described by many authors, among the latest being Barton and Mason (1925), while Hanna and Wolf (1934) reported fibres, öolites, and crystals of barite from the cap rock of Gulf Coast salt domes.

Stalactites, crusts, and mud consisting of barium and strontium sulphate have formed around a brine spring in a mine at Lautenthal in Hartz Mountains. Lattermann (1888) believed that the barium and strontium salts were precipitated by the mingling of the sulphate waters of the mine with the chloride waters, containing barium and strontium, of the spring. It is noteworthy that the concentration of chlorides in the spring waters is nearly three times that in sea water. Other deposits of baritic sinter around springs were reported from British coal mines by Dunn (1877) and from Colorado by Headden (1905). At the latter site, the sinter contained up to 94.6 per cent barite and was markedly radioactive.

ORIGIN OF CONCRETIONS FROM CALIFORNIA SEA FLOOR

Characteristics requiring explanation

The following characteristics of the concretions from the California sea floor seem to be of genetic importance:

1. Localized occurrence on a probable fault scarp
2. Tubular shape of many of the concretions
3. Concentric zoning with higher barite content in outer shells
4. Warty surfaces and nipple-like protuberances
5. Probable greater permeability of flat concretions
6. Presence of fossil Foraminifera
7. Higher computed original porosity of concretions than measured porosity of enclosing mud
8. Relatively high content of strontium
9. Only traces of barium in enclosing mud
10. Abnormally high chlorinity of interstitial water in concretions

11. Lower sodium-potassium ratios in concretions than in mud
12. Lower silica-sesquioxide ratio in concretions than in mud
13. Brownish-gray color of some concretions, indicating oxidation

Concentration of Barite by Organisms

Samoilov in 1917 suggested that Xenophyophora, which are known to have skeletons containing barite granules, were responsible for the formation of concretions found off Ceylon. Andrée extended this suggestion to explain the occurrence of barite nodules off the Kai Islands. Xenophyophora are said to be widely distributed in the tropics, yet only three findings of barite concretions in dredgings are known, one of which, that off California, is outside the tropics. Had the barite of the nodules been originally deposited on the sea floor as the remains of these rhizopods, it would seem that a more wide-spread distribution of concretions would have resulted, and also that appreciable quantities of barite would have been present in muds enclosing the concretions. Moreover, analyses of the concretions from Ceylon and California show a relative abundance of strontium, only traces of which are associated with barite in the skeletons of the Xenophyophora (Schulze, 1905). Even if the original accumulation of barite had been carried out by these organisms, the tubular shape, zoning, and chemical contrast between the concretions and the mud would have required the subsequent migration and concentration of either dissolved or colloidal $BaSO_4$. This was, in fact, pointed out by Samoilov.

Chemical Precipitation from Sea Water

It might be supposed that chemical processes operating in the bottom muds could cause the precipitation of barium sulphate from sea water within or immediately above the sediment. Such precipitation would depend on whether the solubility product of $BaSO_4$ was exceeded. The concentration of barium in sea water is so low that it cannot be determined quantitatively by chemical methods. Since barium is utilized only to a slight extent by organisms, its concentration should bear a constant ratio to the chlorinity as do calcium and sulphate (Lyman and Fleming, 1940). According to Engelhardt's spectrographic examination (1936), the content of barium in sea water is less than 0.03 to 0.08 mg. per liter. He suggests that actually only a half to a tenth of this amount may be present. Taking a value of .005 mg./liter as the most probable one, and combining it with the known sulphate concentration of sea water, there is obtained an ion product for $BaSO_4$ of about $6\ (10)^{-10}$. Since the solubility product of $BaSO_4$ in pure water is about $1\ (10)^{-10}$, this would represent a sixfold supersaturation were it not for the lowered activity of ions in relatively concentrated salt solutions like sea water. The effect of lowered activity is shown by the approximately eight times greater solubility of calcium sulphate in sea-water than in pure water (Fraps, 1902). Barium sulphate itself is said to be about 15 times more soluble in magnesium chloride solutions of ionic strength equivalent to that of sea water than it is in extremely dilute solutions. It thus seems probable that the sea is only saturated or perhaps even undersaturated with $BaSO_4$. In order to cause precipitation, the content of either barium or sulphate must be increased over that prevailing in normal sea water. Such a concentration of sulphate is unlikely in the reducing environment of the bottom muds. Because of the small concentration of barium in the sea, all the barium from about 300 cubic meters would have to be extracted to form a concretion weighing a hundred grams and having 50 per cent barium sulphate. It is difficult to conceive of a motive force which would move such a large volume of water through a small space within the bottom muds. If this origin were effective, then the barite concretions would be a widespread phenomenon.

In 1901, Mackie proposed that the baritic nodules in the Triassic of Elginshire might have been formed by precipitation of barium sulphate during the evaporation of a saline lake. A similar origin was suggested by Meland (1922) for the barite rosettes of Oklahoma. Such a process off the California coast could have taken place only in a closed basin and therefore must have occurred long after the deposition of the muds, because the Foraminifera found within the concretions are typical of those of the open sea of Pliocene times. The barite might be expected to occur not as locally distributed concretions of various shapes but as thin crusts present over a wide-spread area. Other products of evaporation should be associated with the barite had the barium been concentrated in this manner, whereas none are present.

Cementation of Channels by Percolating Waters

Evidence for migrating solutions.—The tubular shape and the concentric zoning of many of the nodules might have originated through the cementation by barite of sediment surrounding a percolating channel. The flat type of concretion might likewise have been developed because of the greater permeability to migrating solutions offered by a thin shelly layer within fine-grained less pervious sediments. Nipple-like protuberances and possibly warty surfaces might have originated through the existence of a system of branching channels. The apparently higher original porosity of the concretions may indicate that moving waters swept out some of the fine-grained constituents of the mud from the channels. The apparently higher original porosity of the concretions may indicate that moving waters swept out some of the fine-grained constituents of the mud from the channels. On the other hand, this may be due to the cementation of a partially uncompacted sediment or to swelling accompanying crystal growth. The absence of barium in the mud indicates that the solutions must have come from an appreciable distance to the points of deposition. Strontium likewise must have been transported to the site, but, owing to its greater solubility, became more widely disseminated before precipitation.

Ground water.—Two types of migrating water may be considered: ground water and ascending juvenile water. Barite deposition from percolating ground water has been proposed by a number of writers as a probable mode of origin for many concretions found on land. If the concretions did originate in this manner, the ground water could not have been largely composed of sea water because of certain chemical characteristics of the concretions. The replacement of sodium by other cations, as shown by the reversal of the sodium-potassium ratio in the concretions as compared with the mud, could not have resulted from the action of sea water in which sodium is a predominant ion. Likewise, the calculated chlorinity of the interstitial water of both the concretions and the mud is much greater than that of normal sea water. Alumina and iron are present in extremely small quantities in sea water, yet these were concentrated in the concretions.

Owing to its high concentration of sulphate ions, sea water cannot dissolve or transport appreciable quantities of barium. Likewise, ground water from meteoric sources passing through marine sediments would probably acquire so much sulphate that it could not dissolve barium-containing minerals. Moreover, the localized occurrence of the concretions off San Clemente Island suggests that any ground water containing barium must have been very restricted areally.

Ascending hot solutions.—In our opinion, a reaction between ascending hot solutions and interstitial sea water of the sediments represents the most probable mode of origin of the concretions. The waters of some hot springs are known to contain appreciable quantities of barium chloride; in fact, many important deposits of barite are of hydrothermal origin (Emmons, 1918). Hot chloride solutions rising through marine sediments would come in contact with interstitial sea water high in sulphate ion, with the consequent precipitation of barium sulphate. Strontium, also commonly found in hot-spring waters containing barium, would have been in part precipitated with the barite and in part transported a greater distance because of the higher solubility of strontium sulphate. Highly concentrated chloride solutions such as those analyzed by Lattermann, might have been responsible for the increase in chlorinity of the interstitial water in the concretions and the adjacent mud. Alumina and iron could have been carried and deposited with the barium and strontium, while replaceable sodium and perhaps some calcium carbonate might have been removed by slightly acid waters in which sodium was not the predominant cation. Such waters could also have carried the radioactive materials present in the concretions. It is well known that ascending hot solutions often escape to the surface in springs along faults, and thus a reasonable explanation is provided for the localized occurrence of the concretions along a probable fault scarp.

Possible Origin of Other Barite Nodules from the Ocean Floor

An interesting comparison may be made between the occurrence of the nodules off California and of those dredged from off Ceylon and off the Kai Islands. In each instance, the concretion locality is situated on or near a probable fault of considerable magnitude, which may have provided an avenue of escape of hot baritic solutions from magma to the surface. Although the exact locality of the concretions described by Jones is not known, the depth reported indicates that they occur along the straight steep slope bounding the western side of Ceylon. (See Feuille A IV of the Carte General Bathymetrique des Oceans, International Hydrographic Bureau, 1938.)

No modern soundings exist in the neighborhood of the locality from which barite nodules were dredged by the Siboga Expedition, but several facts indicate that this occurrence is in a zone of major earth movement. The following quotation is translated from Weber's footnote in French (1902) with reference to the station from which the nodules were dredged:

> "To the north of the principal island of the Basse-Kei group an island has emerged from the bottom of the sea in historic times. This miniature island is situated on a sand bank and is surrounded by a coral bank which extends to Oed Island. The island consists of clay (and not of sand as is commonly the case with coral islands) and one finds also 'some stones, some traces of iron oxide, and fragments of ferruginous manganese'. This composition of the soil, although very remarkable for a coral island, corresponds perfectly in its nature to the bottom of the sea, which I have described. Even though this appears fantastic, I cannot refrain from pointing out this remarkable concordance".

Within a mile of the Siboga locality, the Challenger Expedition dredged

> "several large concretions or fragments of a calcareous rock differing very considerably from the deposit (of blue mud). A section of these concretions resembled in most respects a section of a hardened globigerina ooze from tropical regions and near a continental shore. It is not improbable that these large concretions or rock fragments are hardened portions of a deep sea deposit formed at a much greater depth and subsequently elevated to the position in which they were found, probably by the the same elevation as that which upheaved the neighboring islands." (Murray and Renard, 1891)

The presence of major structural trends near the Kai Islands has also been pointed out by Kuenen (1935).

Summary

During the course of an investigation of the ocean floor geology off southern California, one of a large number of samplings encountered a submarine outcrop which consisted in part of barite concretions. These nodules are variable in size, shape, and surface character, as well as in bulk specific gravity. Many are concentrically zoned, with a hard outer shell surrounding a softer core. Petrographic examination shows that the barite is present chiefly as small radial aggregates of closely interlocking crystals often best developed inside the tests of Foraminifera. Most of the concretions include clay together with minor amounts of coarser detrital grains, but a few contain a much greater proportion of larger particles, chiefly plagioclase, glauconite, and foraminiferal tests. Spectrographic examination shows that barium and strontium are present in relatively large quantities in the concretions but in only minor amounts in the enclosing mud. Three chemical analyses of the nodules show the presence of 62 to 77 per cent $BaSO_4$, the highest amount being in the outer layer of a zoned concretion. The ratios of silica to sesquioxides and of sodium to potassium are lower in the concretions than in the enclosing mud. Bulk specific gravities vary between 2.43 and 3.01, while grain densities range from 3.44 to 3.97. Calculations based on these values show a porosity ranging from 14 to 34 per cent. The average barium sulphate content calculated from the specific gravity is 63 per cent by weight, or 50 per cent by volume. The bulk specific gravity, grain specific gravity, and porosity of the enclosing mud are respectively 1.13, 2.51, and 55 per cent. The calculated chlorinity of the interstitial water in the concretions is 33 parts per thousand, considerably higher than the normal chlorinity of bottom sea water. Examination of the tests of Foraminifera contained in the concretions shows that 68 per cent of the species found do not occur on the present sea floor at the depth of barite outcrop and probably represent an early Pliocene fauna.

It is concluded that the nodules originated by a reaction between hot solutions ascending along a fault scarp and the interstitial sea water of the sediments. The ascending waters are thought to have carried strontium, aluminum, and iron, as well as barium, and to have been low in sodium and pH. A similar origin is suggested for the two other occurrences of barite nodules from the sea floor reported in the literature. This suggestion is supported by the fact that in each instance the concretion locality is situated on or near a fault of considerable magnitude which may have provided an avenue of escape of hot baritic solutions from magma to the surface.

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SCRIPPS INSTITUTION OF OCEANOGRAPHY, LA JOLLA, CALIFORNIA; UNIVERSITY OF SOUTHERN CALIFORNIA, 3518 UNIVERSITY AVENUE, LOS ANGELES, CALIFORNIA

MANUSCRIPT RECEIVED BY THE SECRETARY OF THE SOCIETY, JULY 12, 1950

CONTRIBUTION FROM THE SCRIPPS INSTITUTION OF OCEANOGRAPHY, NEW SERIES, NO. 510.

FORECASTING OCEAN WAVES[1]

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Introduction

One result of the interaction of wind and ocean is the generation of surface waves. Prior to 1940 a few inadequate empirical rules formed the only basis for the prediction of wind-induced waves. A concentrated effort under the stimulus of wartime demands has resulted in the development of relationships which make possible the forecasting of ocean waves from synoptic meteorological data.

As an introductory example, reference is made to the meteorological situation north of the Hawaiian Islands in early January 1947. An intense low-pressure center remained virtually stationary 1000 miles to the northeast of the islands for a period of more than 72 hours (Fig. 1). On January 1 and 2, the winds in an area extending from 500 to 1200 miles north of the islands were force 8–10 and direction N-NNW for a period of 36 hours. This area comprised the *fetch* and computations based on wind velocity, duration, and the forecasting relationships give a wave height of 38 ft and a period of 11.3 sec at the southern boundary [1]. The characteristics of the wind waves which are in the process of generation in such a fetch are referred to as *state of sea* or simply *sea*. After the wind waves left this particular area of direct influence of intense winds, they continued onward as *swell* through a region of relatively weak winds, and reached Hawaii in 28 hours after having traveled a distance of 600 nautical miles. Over this *decay distance* the height of the significant waves decreased and the period and length increased. Computations yield a swell of height 22 ft and period 14 sec, and available observations compare favorably with these calculations. Further computations show the swell reaching Palmyra Atoll, which is 900 miles south of Hawaii, with a height of 12.5 ft and a period 17 sec after an additional travel time of 29 hours.

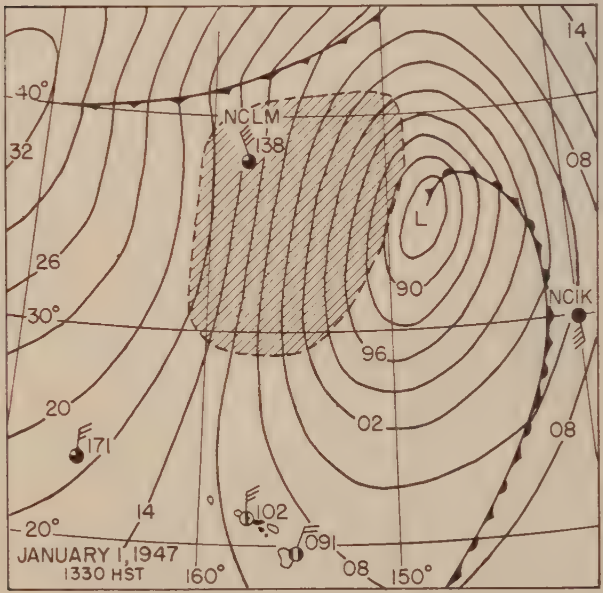

Fig. 1.—Weather map for 1330 Hawaiian Standard Time, January 1, 1947. The shaded area represents the fetch.

The damage in Hawaii was estimated at between one and two million dollars. Three waves are reported to have inundated low-lying Cooper Island in the Palmyra group. Although these wave conditions are extreme for Hawaii and Palmyra, wave damage in general is by no means rare. Damaging waves may even move from one hemisphere to another. In April 1930, more than 20,000 tons of superstructure stone were displaced from the Long Beach, California, breakwater by the action of swell which in all probability had its origin in the "Roaring Forties" of the South Pacific Ocean. The "rollers" of St. Helena and Ascension, which cross the equator after moving from the North Atlantic, have been famous since at least 1846, when thirteen vessels were driven from their moorings and wrecked on the shores of St. Helena. Reports of the disaster indicate that waves broke seaward of the vessels at a depth of around 20 m which denotes that breaker height was approximately 50 ft.

The primary motivation for the development of a wave-forecasting method has been the fact that waves are a nuisance. This problem came into particular prominence during the planning in 1942 of the invasion of North Africa. In that year, Instructor Commander C. T. Suthons, R. N., began an investigation of wave-forecasting techniques in England, and the same problem was studied in the Oceanographic Section, Directorate of Weather, Headquarters, Army Air Forces. The study was continued at Scripps Institution of Oceanography under Air Force and, later, Navy support, and in 1943 the method which was used throughout the war had in essence been developed [8]. Although oceanographers played an important role in the development of forecasting methods, the application is best carried out by meteorologists.

Since waves represent the effect of the wind integrated over time and distance, forecasts of waves can be made from a knowledge of only the large-scale features of the wind distribution. Such forecasts are likely to be made more easily and with greater certainty than most types of meteorological forecasts.

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[1] Contribution from the Scripps Institution of Oceanography, New Series No. 511. Many of the results discussed here are based on research supported by the Office of Naval Research, Navy Department, under contract with the University of California.

The present status of wave forecasting is that there are available methods which permit useful predictions of certain wave characteristics from synoptic meteorological observations. The theoretical basis of the methods does not adequately explain the physical mechanism of wave generation and decay. We shall consider wave forecasting, the deficiencies of the methods, and some of the unsolved problems.

Sea, Swell, and Surf

The categories *sea*, *swell*, and *surf* form a natural division of the topic of wave forecasting. The latter, or more generally, the transformation of waves in shallow water, is dealt with by methods which are somewhat different from those used in the study of sea and swell. The essential features of the surf problem have been accounted for physically, whereas this is not the case for sea and swell, as previously mentioned. Sea is determined by the nature of the winds, and the forecasting of sea depends therefore upon the current and predicted synoptic meteorological situation. Swell depends to a lesser extent upon the synoptic situation, but its characteristics can still be altered by a following or an opposing wind during the course of decay. Surf is determined by factors which are largely nonmeteorological, and we confine our consideration of surf to this section, where we note some of the important physical factors in the problem.

As waves move into shallow water the wave length and wave velocity decrease. Waves moving at an angle to the bottom contours are subject to refraction. The wave crests tend to orient themselves parallel to the bottom contours. Changes in wave-crest orientation are associated with convergence and divergence of energy along the crest [11]. As a result, waves over a submarine canyon are relatively low compared to waves on either side of the canyon; the pattern is reversed for a submarine ridge. These changes can all be quantitatively accounted for by the linear-wave theory, assuming conservation of energy and constancy of wave period [22]. An exception occurs where the waves travel over great stretches of shallow water such as exist along the coast of the Gulf of Mexico and the shelf east of Long Branch, New Jersey. In such cases the effects of bottom friction [14] and percolation [13] should be taken into account.

As the waves approach the breaking point the height increases rather suddenly, and the wave breaks at a depth approximately equal to $\frac{4}{3}$ the wave height. Adequate predictions can be based on the application of the solitary-wave theory [12]. Waves breaking at an angle to the shore set up longshore currents whose average velocity can be roughly estimated when bottom contours are straight and parallel [15]. In the case of nearly normal wave approach, longshore currents are variable in direction and form an integral part of a system of currents, called *rip currents* [19], which include narrow zones of fast flow away from shore. Active research is being conducted on the near-shore circulation [19], including rip currents, on orbital velocities, and on the important role played by waves, particularly breakers, in beach erosion and in the design of engineering structures.

Although a number of characteristics of surf are predictable if the deep-water wave characteristics and the bottom topography are known [9], it must be noted that the basic relationships apply only approximately, and even large deviations are to be expected. More research on surf is indicated, particularly on the problem of the mechanism of breaking.

Forecasting Significant Waves

The notations given below will be used in the discussion which follows.

F—length of wind fetch (subscript F denotes value of variable at end of fetch);
D—decay distance (subscript D denotes value of variable at end of decay distance);
H—wave height;
C—phase velocity of wave;
T—wave period;
L—wave length;
δ—H/L (wave steepness);
E—mean energy of wave per unit area;
x—horizontal distance coordinate;
t—time;
t_d—duration time of wind;
U—wind velocity at about 8 m above surface;
β—C/U (wave age);
τ—tangential stress of wind on sea surface;
u_0'—mean surface mass transport velocity;
R_N—mean rate of energy transfer to wave as a result of normal wind pressure;
R_T—mean rate of energy transfer to wave as a result of tangential wind stress;
g—acceleration of gravity;
s—sheltering coefficient;
ρ—density of air;
γ^2—resistance coefficient applicable to wind.

The outstanding characteristic of sea and swell is its irregularity, and a complete description of the sea surface requires the introduction of statistical terms. Nevertheless, a practical purpose can be served by dealing only with the most prominent, or "significant," waves. A definition of the term "significant" is given in the following section. One of the major achievements of wartime wave forecasting was the development of operationally useful methods, one with a theoretical-empirical basis [24], and the other primarily empirical [20]. We next consider the results and basis of the first method, and make a brief comparison with the second.

Observers have noted that as the wind blows over a limited fetch, the wave height and period over the upwind part of the fetch reach a steady state after a limited interval of time. As time passes the steady-state region expands over the whole fetch. The wave height and period at the end of the fetch are determined from the wind velocity, fetch, and duration. The relationships given below, in terms of nondimensional parameters, follow from the forecasting theory.

Steady state:

$$gH_F/U^2 = f_1(gF/U^2), \quad (1)$$

$$C_F/U = f_2(gF/U^2); \quad (2)$$

Transient state:

$$gH_F/U^2 = f_3(gt_d/U), \quad (3)$$

$$C_F/U = f_4(gt_d/U). \quad (4)$$

Height and period of swell at the end of the decay distance and travel time are determined from the decay distance and the period at the end of the fetch according to:

$$H_D/H_F = f_5(D/gT_F^2), \quad (5)$$

$$T_D/T_F = f_6(D/gT_F^2), \quad (6)$$

$$t_D/T_F = f_7(D/gT_F^2). \quad (7)$$

Relationships (1)–(7) are translated into practical graphs for use in forecasting[2] (examples are presented in Figs. 2 and 3).

The basis of the theory is the development of equations which express the energy budget between wind and waves. Use is made of results from two hydrodynamical theories of irrotational waves: (1) the Airy theory of waves of small amplitude, and (2) Stokes' theory of waves of finite amplitude. Certain constants which occur in the solution are evaluated empirically.

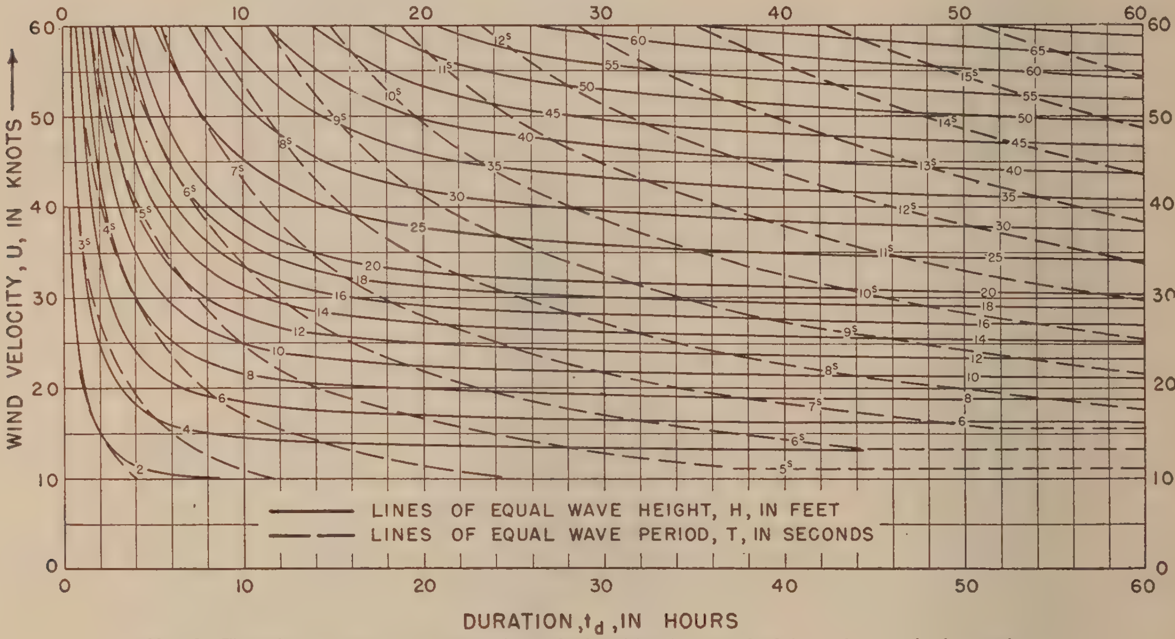

FIG 2—Transient state wave-generation relationships in practical form for use in forcasting.

The assumption is made that energy is transferred from wind to waves by normal pressure and tangential stress. Following Jeffreys, the expression used for the mean rate of energy transfer per unit area as a result of normal wind pressure is

$$R_N = \pm \frac{\pi^2}{2} s\rho(U - C)^2 \delta^2 C, \quad (8)$$

where the sign is positive for $U > C$ and negative for $U < C$. Thus, a transfer expression which depends upon variations in pressure along the surface is introduced, although use is made of hydrodynamical theories which assume constant pressure along the surface.

For the tangential stress, the form

$$\tau = \gamma^2 \rho U^2, \quad (9)$$

where $\gamma^2 = 2.6 \times 10^{-3}$, is introduced with the understanding that wind velocities are great enough so that the sea surface is hydrodynamically rough. The expression for R_N is derived using the horizontal component of particle velocity at the surface from the Airy theory, but on this basis no energy is transferred by tangential stress. However, if the average surface mass transport velocity, $u_0' = \pi^2\delta^2 C$, from the Stokes theory is utilized, the mean rate of energy transfer per unit area by tangential stress is

$$R_T = \frac{1}{L}\int_0^L \tau u_0' \, dx = \pi^2 \rho \gamma^2 \delta^2 C U^2, \quad (10)$$

and on the basis of this expression a transfer of energy from wind to waves is possible even if the waves move faster than the wind. Further investigation of this point is indicated because if the difference between the wind velocity and the horizontal component of particle velocity is introduced in the expression for τ, seemingly a more accurate formulation of the transfer expression, no energy is added on the basis of either the Airy or the Stokes theory if the waves move faster than the wind. The validity of Stokes' expression for mass transport in the case of waves on a rotating globe has also been questioned.[3]

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[2] R. S. Arthur, "Revised Wave Forecasting Graphs and Procedures." *Scripps Institution of Oceanography Wave Report No. 73*, March 1948 (unpublished). These forecasting relationships, as revised according to [24], are to be included in a forthcoming manual on wave forecasting to be issued by the Hydrographic Office.

If the waves are conservative, that is if they maintain their identity, the knowledge from theory of the way in which energy advances with the wave form leads to the following differential equations:

Steady state:

$$\frac{C}{2}\frac{dE}{dx} + \frac{E}{2}\frac{dc}{dx} = R_T \pm R_N; \qquad (11)$$

Transient state:

$$\frac{dE}{dt} + \frac{E}{C}\frac{dC}{dt} = R_T \pm R_N \qquad (12)$$

where the positive sign is used for $C \leqq U$ and the negative sign for $C > U$. Actually the waves comprising sea cannot be conservative and the equations apply at best only approximately.

Since the wave energy is related to the wave height, the two unknowns in the equations above may be considered as wave height and wave velocity and the knowns as distance and time. An additional equation is obtained by assuming that the energy transferred from the wind is divided in a certain fixed manner between the energies required to increase wave height and wave period. The solution of the resulting system of differential equations leads to a relationship between wave steepness and wave age,

$$\delta = f(\beta) \qquad (13)$$

and, finally, to the relationships (1)–(4) above.

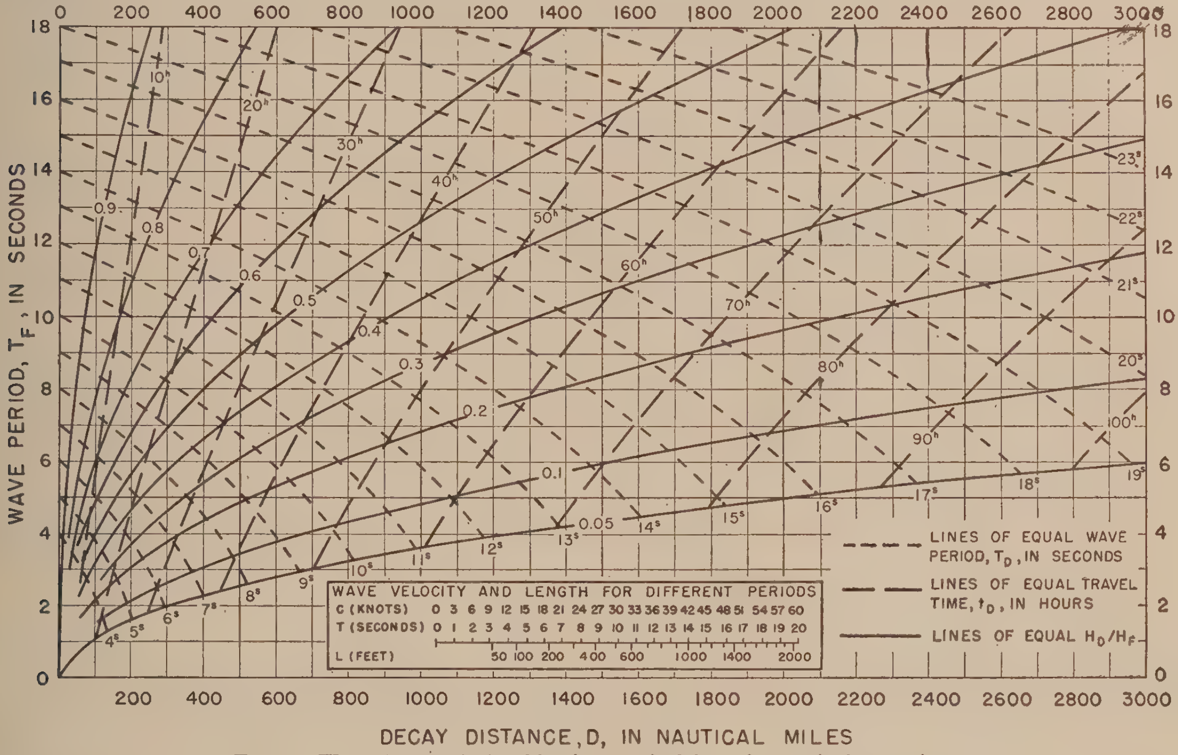

FIG. 3.—Wave-decay relationships in practical form for use in forecasting.

The relationship between δ and β is particularly useful in comparison with wave observations. Many of the observations available for the first checking of the forecasting relationships were inadequate in that either duration time or fetch or both were missing. Most observations are sufficiently complete for the computation of wave steepness and age. Certain constant parameters appearing in the equation are evaluated by fitting the analytical expression (13) to the available observations. The resulting relationship (solid line curve, Fig. 4) gives a satisfactory fit.

Waves leaving the fetch and advancing as swell through a region of calms lose energy by the normal pressure effect of air resistance, but no effect of tangential stress need be considered. The solution of the equation expressing the energy budget of swell yields an increase of wave period during decay and a decrease of wave height, and these facts are in agreement with observations.

Sverdrup [21] compares the decay of swell to the advancement under the influence of air resistance of a train of impulsively generated waves and shows that the period increase is explicable as a result of selective attenuation. The comparison suggests that travel time be computed on the basis of the decay distance and the group velocity of the swell at the end of the decay distance. The effect of a following wind during decay is to give lower swell arriving earlier, and the effect of an opposing wind is the opposite. The results for travel time, following wind, and opposing wind are incorporated into the forecasting method.

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[3] F. Ursell, "The Theoretical Form of Ocean Swell on a Rotating Earth." Admiralty Research Laboratory, A.R.L./R.6/1.03.41/W, February 1947 (unpublished).

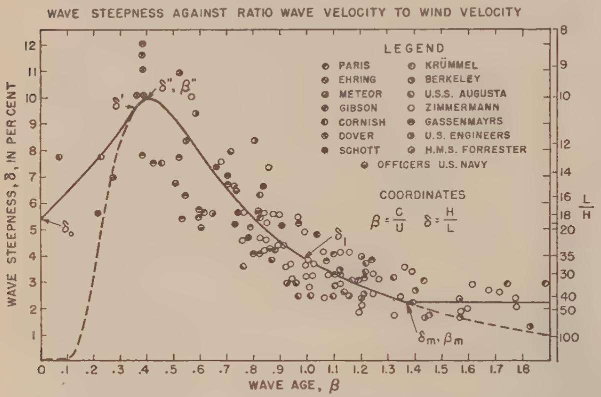

Fig. 4.—Wave steepness plotted against wave age. The dashed lines represent the part of the theoretical relationship which must be modified to conform to empirical evidence.

Groen and Dorrestein [7] attribute the decay and the period increase of swell to a selective damping by eddy viscosity. The eddy-viscosity coefficient used depends on the size of the systems under consideration, and the coefficient is larger for long waves than for short ones. Groen and Dorrestein point out that it is improbable that the values of the sheltering coefficient would be the same for swell and wind waves as Sverdrup and Munk [24] have assumed.

Table I. Predicted and Observed Wave Characteristics

	Per cent of cases
Predicted height within 1 ft of observed height	53
Predicted height within 2 ft of observed height	80
Predicted period within 2 sec of observed period	63
Predicted arrival time within 6 hr of observed time	69

Isaacs and Saville [10] have compared forecasts made according to the method in its present form with records from wave meters at Point Sur, California, and Heceta Head, Oregon. The results of the comparison for a total of more than 200 forecasts for each station during the period April to December, 1947, are given in Table I. The predicted heights are appropriately corrected for the transformation from deep water to the position of the wave meter. They do not show any tendency to be higher or lower than the observed heights. The predicted arrival times, however, show a tendency to be too early and the periods to be too low.

According to Isaacs and Saville, "97 per cent of the recorded significant *increases* in wave height were forecast, but 23 per cent of the forecast wave trains failed to arrive. The rather large proportion of non-arrivals apparently resulted from the erroneous selection of fetches. . . ." They conclude that the forecasting technique "results in a high degree of reliability for forecasting the arrival of significant increases in wave height, and prognosticating the wave heights," but that "the forecast of wave period and arrival time of the peaks of the wave trains does not display the same degree of reliability. . . ." Bates [3] reviews the forecasting of sea, swell, and surf for landing operations in World War II and concludes that the forecasts were basically correct.

Suthons [20] presents graphs for the forecasting of sea and swell, but the empirical data on which they are based and the exact methods of preparation are not indicated. Predicted wave periods for sea are longer from these graphs than from the first method, and wave heights lower. If a δ,β-relationship is derived from Suthons' graphs, the agreement with the observational data mentioned above (Fig. 4) is not good over a wide range of β values. Suthons attributes the increase in wave period to the downward transport of wave energy by molecular and eddy viscosity, but no quantitative discussion of the mechanism is presented.

The Wave Spectrum

The great complexity of the waves in the sea obscures the exact meaning of earlier wave observations which form the empirical basis for the forecasting methods discussed in the preceding section. Only recently has it been possible, by analyzing records from pressure-type wave meters, to clarify the relation of the predicted wave height and period to the irregular pattern actually recorded.

An individual wave record shows a wide range of heights and periods. For many practical applications, such as the landing of craft, wave action on structures, and sand movement, only the heights and periods of the higher waves in the record are significant. The terms *significant wave height* and *significant wave period* have accordingly been defined as the average height and period, respectively, of the highest one-third of the waves, after ripples and waves of height less than one foot are eliminated from consideration [23].

Experience shows that observers who attempt to determine visually the characteristics of waves tend to record heights and periods which are approximately those of the significant waves rather than of the average waves. Since the forecasting method is based on such visual observations, one might expect that the predicted wave heights and periods are to be considered significant heights and periods. This expectation has subsequently been confirmed [10].

The characterization of a wave record in terms of the significant waves gives a useful description of the record.[4] Wiegel [25] finds that the daily average height of the highest ten per cent of the waves bears a relatively constant relationship to the significant height at the locations on the Pacific Coast of the United States. This fact is of practical importance because less time is required to compute the average for the highest ten per cent. A good correlation between the maximum waves recorded each day and the significant waves is also noted, and Seiwell [17] finds at Cuttyhunk and Bermuda that the ratio of the daily average height of all waves to the highest one-third is relatively constant. These results (Table II) taken collectively indicate that in general a similar *distribution* of wave heights prevails in the waves generated in different storms although the absolute magnitude varies.

TABLE II. RATIOS OF MEAN WAVE HEIGHT AND OF AVERAGE OF HIGHEST 10 PER CENT TO SIGNIFICANT WAVE HEIGHT

	Observation Point					
	Scripps[4] (swell)	Point Sur [25]	Heceta Head [25]	Point Arguello [25]	Cuttyhunk [17]	Bermuda [17]
Interval over which averages formed..................	46 waves	three 20-min intervals per day			2-min intervals	
Ratio of mean to significant.........	0.67				0.64	0.64
Ratio of highest 10% to significant......		1.27	1.30	1.30		

A more detailed interpretation is obtained by subjecting the records to harmonic analysis. Barber and Ursell [2] have pioneered in the development of instruments for obtaining the Fourier amplitude spectrum. The spectra are taken to indicate that a storm produces a mixture of trains of waves of all lengths up to a maximum which depends on the greatest wind strength. The component trains act independently during decay, and each travels at the group velocity appropriate to its period. In an individual spectrum at a very distant station the swell covers a narrow range of periods, but at a closer station the wave band is wider and broadens rapidly toward shorter periods. Seiwell and Wadsworth [18], on the other hand, take issue with such an interpretation of the component periods in the Fourier amplitude spectrum. From a computation of the autocorrelation function they reach the following rather surprising conclusions which are quoted from their summary:

> (1) Periodogram analyses performed on oceanic wave records do not appear to give correct geophysical information. The numerous wave periods, and bands of periods, indicated by this type of analysis do not necessarily possess physical significance.
>
> (2) Application of the hypothesis of generalized harmonic analyses to western North Atlantic wave records indicates that ocean wave patterns are not complex interference patterns resulting from combinations of many wave frequencies, but frequently consist of a single sinusoidal wave on which is superimposed an oscillatory component. . . .

This question of the interpretation of records is fundamental in the consideration of wave generation and propagation, and it merits further study.

Problems in Forecasting

Three main stages in the study of forecasting ocean waves from storms can be recognized. In the earliest stage the forecasting was based on empirical "engineering rules," mutually inconsistent and often incomplete. The well-known Stevenson's law, for example, relates wave height to fetch without regard to wind speed. The second stage was the development during World War II of consistent, dimensionally correct relationships. These relationships have made it possible to forecast the significant waves to an accuracy sufficient for many practical applications. Most of the foregoing discussion deals with this stage of the development. The relationships are strengthened by the application of hydrodynamic theory, although the theoretical basis is not at all secure. The third stage, and one which we are now entering, centers about the British studies of the wave spectrum [2, 5], and some recent attempts to forecast the entire spectrum [4].

According to Deacon [4],

> The width of the spectrum when waves are being generated by a rising wind suggests that the energy begins to be distributed over a range of wave lengths as soon as the waves are formed, some being communicated to the longer wave lengths before the shorter ones are fully energized. Each spectrum has an *optimum band* in which the waves are highest. Waves shorter than this optimum period are lower, presumably because they have a smaller capacity for absorbing energy without becoming unstable; and longer waves are lower, probably because their speed, which is nearly equal to that of the wind, allows them less opportunity of absorbing energy. . . . The period of the highest waves is approximately 25 per cent less than the period of the longest waves.

From this point of view the forecasting of significant waves is closely related to the forecasting of the optimum band. An increase in significant wave height with fetch, or with wind speed, corresponds to an increase in the maximum energy contained in this band, and an increase in the period of the significant waves represents a shift of the optimum band towards longer periods. Since the characteristic of this optimum band depends closely on the character of the component wave trains longer and shorter than those of the band, it is not possible to develop a satisfactory physical theory for forecasting the optimum band without regard to the remaining portion of the spectrum. Nor is it desirable to do so, for there are many practical problems for which the character of the optimum band is only incidental. In the study of the acoustic and optical properties of the sea surface the short-period portion of

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4. W. H. Munk, "Proposed Uniform Procedure for Observing Waves and Interpreting Instrument Records." *Scripps Institution of Oceanography Wave Report No. 26*, December 12, 1944 (unpublished).

the spectrum is the important one. In the problem of storm tracking we are most interested in the longest periods present, as those travel most rapidly.[5] It is therefore desirable to divorce from the problem of wave forecasting the selection of that particular portion of the spectrum which happens to be important to a definite application.

The derivation of the physical laws governing the growth of the component wave trains under wind action remains the outstanding theoretical problem in the development of a method for forecasting the wave spectrum. The problem promises to be a difficult one for at least two reasons: (1) the limitations on the growth of the shorter waves imposed by stability considerations introduce a nonlinearity into the problem; (2) to the extent to which the lower, shorter waves are sheltered from the wind by the large waves, the energy budgets of the component wave trains are not mutually independent.

The problem of forecasting the transformation of the swell traveling through the region of decay also resolves itself into the problem of forecasting the change in the spectrum of the swell. The observed increase in the period of the significant swell is the result of the relatively rapid attenuation of the short-period components. One possible mechanism is provided by the viscous effects of the water, according to which the dissipation of energy is inversely proportional to the fourth power of the wave period. It can, however, easily be demonstrated that the effect of viscosity is several orders of magnitude too small to explain the observed transformation. Sverdrup [21] has, however, demonstrated that the selective attenuation resulting from the air resistance on waves traveling through regions of calm (equation (8) with $U = 0$) provides a possible mechanism for selective attenuation. Groen and Dorrestein suggest that selective damping by eddy viscosity is the mechanism. Further study is indicated.

It should also be noted that laws governing the generation of waves at low wind speed can be expected to differ from those governing the generation at moderate and high speeds. The reason lies in the character of the sea surface, which appears to be hydrodynamically smooth at wind speeds less than 6 m sec^{-1}, and hydrodynamically rough at wind speeds exceeding 7 m sec^{-1} [16]. Equation (9) and all subsequent development is based on the assumption of a rough sea surface.

In addition to the more fundamental problems mentioned above, there remain many problems of practical applications. Among the more important ones is the prediction of waves and swell from a tropical storm. The rules of thumb which have been established[6] do not in all cases lead to adequate forecasts.

Most of the actual testing of wave forecasting methods has been carried out for west-coast situations. Forecasting for an east coast offers some special problems, and these are being investigated by the Department of Meteorology, New York University, under the sponsorship of the Beach Erosion Board, and by the Woods Hole Oceanographic Institution [6].

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OCEAN WAVES AS A METEOROLOGICAL TOOL

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Reprinted from the

COMPENDIUM OF METEOROLOGY

Published by the

AMERICAN METEOROLOGICAL SOCIETY
Boston, Massachusetts

This publication has been made possible through support and sponsorship extended by the Geophysics Research Division of the Air force Cambridge Research Center under Contract No. W 28-099 ac-399. It is published for technical information only and does not represent the recommendations or conclusions of the sponsoring agency.

OCEAN WAVES AS A METEOROLOGICAL TOOL[1]

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Introduction

Since ancient times seafaring men have recognized the significance of ocean waves as a sea-borne storm warning. However, their interpretation was intuitive, based upon the experience gained in a lifetime at sea.

The first attempt to apply this ancient art as an aid in weather forecasting appears to have been made in New Zealand around the turn of the century.[2] Yet no *quantitative* methods were developed until World War II. We shall describe the three general methods which present themselves at this time. Each of these has its advantages and disadvantages, but it is too early to state whether these methods will find widespread application.

The Height-Period Method Applied to Visible Swell

This method is based on the relationships established for forecasting sea and swell from weather maps [15, 16].[3] It consists of computing the wind speed U in a storm area, the distance D from the storm area, and the travel time t_D of a swell, making use of measurements of the swell height H_D and period T_D. A discussion of these quantities is found in another paper.[3] Wave height and period refer to deep water, and to the *significant* waves, that is, the average of the highest one-third of all waves present.[4] Observations from shipboard can therefore be taken without further modification. In the case of land-based observations the wave *period* can be determined at any depth since it does not change as waves enter shallow water. Along steep coastlines or exposed beaches with simple bottom topography the deep water wave *height* can, for practical purposes, be taken as the wave height one or two wave lengths outside the breaker zone. Otherwise it is necessary to take into account, by means of specially constructed "refraction diagrams" [7, 12], the effect of bottom topography and of the configuration of the coastline.

The nondimensional relationships given below follow from the forecasting theory [16]:[5]

$$\frac{U^2}{gH_D} = \frac{1}{2\pi}\,\frac{1}{\delta_F\beta_F^2}\left(\frac{\delta_F}{\delta_D}\right)^{.57}, \tag{1}$$

$$\frac{D}{gT_D^2} = 1.72 \times 10^3\left[1 - \left(\frac{\delta_D}{\delta_F}\right)^{.429}\right], \tag{2}$$

$$\frac{t_D}{T_D} = 2.16 \times 10^4\left[1 - \left(\frac{\delta_D}{\delta_F}\right)^{.429}\right], \tag{3}$$

$$\delta_D = \frac{2\pi}{g}\,\frac{H_D}{T_D^2}, \tag{4}$$

$$\delta_F = \delta_F(\beta_F), \tag{5}$$

$$\beta_F = \beta_F(gt/U), \tag{6}$$

where g is gravity, and t the storm duration. The relationships (5) and (6) are very complicated analytically, and are here presented in graphical form (Fig. 1). Equations (1) to (6) contain seven unknowns, and the quantities U, D, and t_D are therefore not uniquely determined from measurements of swell height and period. To obtain a complete solution a relation

$$t = t\,(U) \tag{7}$$

will be assumed between the duration of the storm and its intensity, based on the common experience that high winds are usually of short duration. For two specific relationships, a storm of unusual duration (line A in Fig. 2 inset), and a short-lived storm (line B), equations (1) to (7) have been solved and the results shown graphically (Fig. 2), using practical units. The examples in Table I illustrate that D and t_D do not depend very critically upon the nature of the relationship $t(U)$ and can be determined with greater certainty than U. To obtain greater accuracy the forecaster may attempt an interpolation between Cases A and B, based on his experience with the duration of storms over particular regions. It should be noted that the results obtained become increasingly uncertain as the distance between storm and observer becomes greater.

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[1] Contribution from the Scripps Institution of Oceanography, New Series No. 512. Many of the results discussed here are based on research carried out for the Hydrographic Office, the Office of Naval Research, and the Bureau of Ships of the Navy Department, under contract with the University of California.

[2] Prof. C. E. Palmer, in a letter to the author, writes, "In the early days of weather forecasting in New Zealand (towards the end of the last century) no information from Australia was available, consequently the only meteorological warning of storms coming from the west was the local fall in the barometer. In an endeavor to get more advanced warnings, Captain Edwin, who was then in charge of a very small weather forecasting organization in the Marine Department, used the observations of sea and swells from light houses to supplement the data on the synoptic maps. These old maps are still in the archives of the New Zealand Meteorological Service and I have studied them with some interest because the reconstruction of the storm positions and tracks by means of the ocean observations seems remarkably good."

[3] Consult "Forecasting Ocean Waves" by W. H. Munk and R. S. Arthur, pp. 1082–1089 in this Compendium.

[4] In estimating wave heights from visual observations there is a tendency to arrive at values well in excess of the mean heights for all waves present. The definition of significant waves given above has been found in accord with the estimates of most observers.

[5] Equation (3) has been revised according to equation (1) in R. S. Arthur, "Revised Wave Forecasting Graphs and Procedure." *Scripps Institution Wave Report 73*, March 1948 (unpublished).

For a discussion of the assumptions underlying the foregoing equations the reader is referred to the original paper [16]. The advantage of this method is that for shipboard observations, or for exposed and steep coasts, it permits a rapid determination of the storm distance and a rough estimate of the storm intensity without the need of special wave-measuring equipment. In this sense the method was first used during World War II by Capt. D. F. Leipper, AAF, as an aid in forecasting the arrival of intense storms in the Aleutian area. In many instances the arrival of heavy swell preceded all other indications of the storm. From a climatological point of view this method can be applied by "mapping" on an H_D,T_D-diagram typical meteorological situations associated with wave conditions in certain areas (Fig. 3).

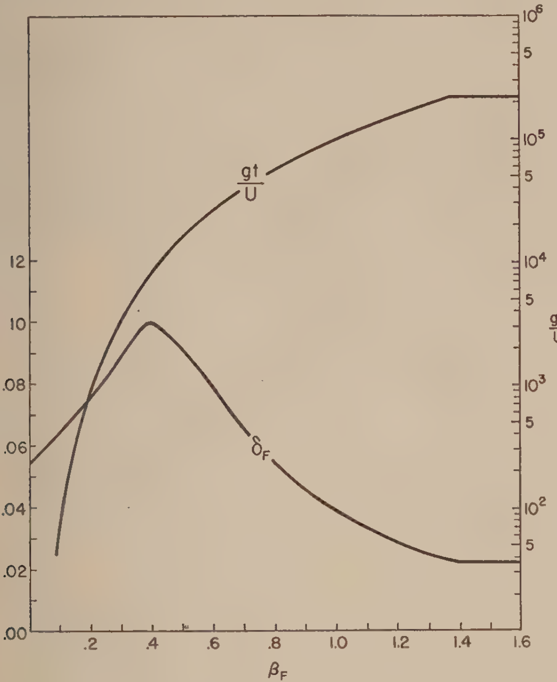

FIG. 1.—Plot of equations (5) and (6) relating wave steepness δ (height/length), wave age β (wave velocity/wind velocity), wind speed U, and wind duration t. Subscript "F" refers to values at end of fetch. (*From Sverdrup and Munk* [16], *Figs. 5 and 7.*)

The principal disadvantage of this method is the slow velocity of the significant waves. As a result the information concerning storm location and intensity may be several days old before the waves reach shore.

The Frequency-Spectrum Method Applied to Forerunners of Swell

The limitations outlined above can be overcome in part by dealing with the low, long, imperceptible waves which precede the visible swell. Since these waves are only a few inches high it is not possible to apply simple, visual methods of observation, but the advantages involved often appear to justify the use of special instrumental techniques.

In the first place, the forerunners travel considerably faster than the visible swell. On the basis of instrumental observations now available [1] the period of the forerunners may reach 25 sec, compared to 12–13 sec as a typical maximum period for the swell. The corresponding group velocities with which the disturbance created by a storm is effectively propagated by surface wave motion are of the order of 900 nautical miles per day for the forerunners, in constrast with 400 miles per day for the swell.

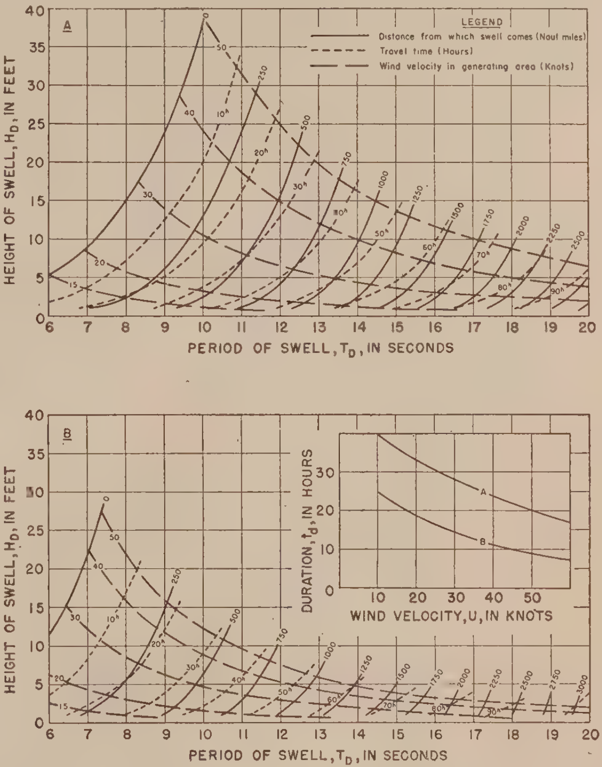

FIG. 2.—Distance from which swell comes, travel time, and wind velocity in generating area as functions of observed height and period of swell. The upper figure is drawn for a long-lived storm, the lower figure for a short-lived storm. The assumed relation between wind speed and duration for these two cases is shown in the inset. (*From Sverdrup and Munk* [16].)

TABLE I. SAMPLE CALCULATIONS FOR A STORM OF UNUSUAL DURATION (CASE A) AND A SHORT-LIVED STORM (CASE B)

H_D (ft)	T_D (sec)	Storm duration (see inset, Fig. 2)	D (naut. mi)	t_D (hr)	U (knots)
6	12	Case A	700	38	30
		Case B	825	45	45

A second advantage of the "frequency-spectrum method" over the "height-period method" is that travel time and storm distance are *uniquely* determined from a knowledge of wave periods. The need for measuring wave height is eliminated.

Instrumentation. Shore-based instruments for recording ocean waves have been in existence for many years.

Most of the older instruments recorded the elevation of the sea surface against time by some suitable arrangements of floats. During World War II very effective methods were developed which derive from the underwater pressure fluctuations induced by the surface waves. It is curious that this mode of attack should have been initiated independently in Great Britain and the United States. An early model developed by the Mine Design Department, British Admiralty, has been in operation at Pendeen, near Lands End, England, since 1944. In the United States the development of wave instruments has been carried out chiefly at the Woods Hole Oceanographic Institution and at the Department of Engineering of the University of California. In an early model designed by M. Ewing the recording apparatus was contained directly in the underwater unit. Later, units recording on shore were installed near Cuttyhunk, Massachusetts, and on the island of Bermuda [8]. A number of shore recording models have been developed at the College of Engineering, University of California [6], and these have been installed at Quillayute River, Washington; Heceta Head, Oregon; Point Cabrillo, Point Sur, Point Arguello, Oceanside, and La Jolla, California; and on the island of Guam.

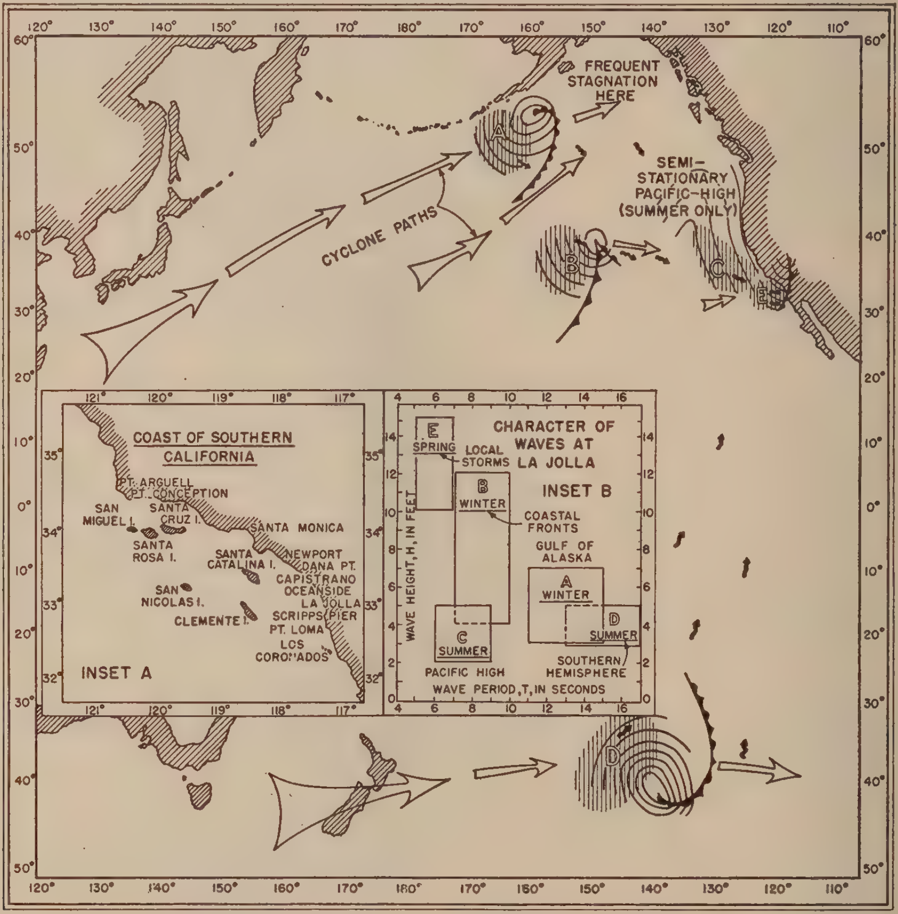
120°
130°
140°
150°
160°
170°
180°
170°
160°
150°
140°
130°
120°
110°
60°
50°
40°
30°
20°
10°
0°
10°
20°
30°
40°
50°
FREQUENT STAGNATION HERE
SEMI-STATIONARY PACIFIC-HIGH (SUMMER ONLY)
CYCLONE PATHS
A
B
C
D
E
COAST OF SOUTHERN CALIFORNIA
PT. ARGUELL
PT. CONCEPTION
SAN MIGUEL I.
SANTA CRUZ I.
SANTA MONICA
SANTA ROSA I.
SANTA CATALINA I.
NEWPORT
DANA PT.
CAPISTRANO
OCEANSIDE
LA JOLLA
SCRIPPS PIER
PT. LOMA
LOS CORONADOS
SAN NICOLAS I.
CLEMENTE I.
INSET A
121°
120°
119°
118°
117°
35°
34°
33°
32°
CHARACTER OF WAVES AT LA JOLLA
INSET B
SPRING
LOCAL STORMS
WINTER
COASTAL FRONTS
GULF OF ALASKA
SUMMER
PACIFIC HIGH
SOUTHERN HEMISPHERE
WAVE HEIGHT, H, IN FEET
WAVE PERIOD, T, IN SECONDS
4
6
8
10
12
14
16
0
2
4
6
8
10
12
14

Fig. 3.—Origin of waves reaching La Jolla, California. The capital letters on the large chart represent typical meteorological situations, which give rise at La Jolla to waves of heights and periods shown in inset B. Inset A is a chart of the region near La Jolla on an enlarged scale. The shaded areas on the large chart represent typical fetches, that is, areas where the waves are generated. The isobaric pattern and the nature of the meteorological fronts are also indicated. The large open arrows represent typical paths of the storm systems. The wavy arrows indicate the direction of the waves leaving the storm systems. The figure cannot represent the nature of the meteorological situations with any degree of accuracy, but it is supposed to illustrate how different meteorological situations can be identified by the height and period of the waves with which they are associated. (*From Munk and Traylor* [12].)

Although the various instruments differ in many important aspects, the following principles are common to most wave instruments of the underwater pressure type and should be understood for a proper interpretation of the records. Surface waves induce pressure fluctuations in the entire column of water between the surface and the sea bottom (Fig. 4). For any given wave height and depth of water, the amplitude of these fluctuations depends on the wave period in such a manner that waves of very short period are virtually eliminated. The underwater unit measures the deviation of the fluctuating pressure at the sea bottom from the mean hydrostatic pressure. A "slow leak" in the underwater unit eliminates the effect of tides and other very long waves. The pressure fluctuations are converted into electrical modulations, which are transmitted through a cable to a shore recorder. Finally the records are subjected to a harmonic analysis by a special instrument [2]. The natural wave spectrum is therefore modified in three stages: (1) waves of short period are removed by hydrodynamic filtering; (2) waves of very long period are removed by the slow leak in the underwater unit; (3) the remaining record is broken down further by harmonic analysis.

Hydrodynamic filtering is particularly adapted for extracting the low forerunners from the complex pattern of the sea surface. The response characteristics of this filter can be expressed by the ratio $\Delta P/\Delta P_0$ of the amplitude of the pressure fluctuation at the bottom to that just beneath the surface. Let h designate the water depth, L the wave length, T the wave period, and g the acceleration due to gravity. The length L can be eliminated between the equations

$$\frac{\Delta P}{\Delta P_0} = \frac{1}{\cosh(2\pi h/L)}, \qquad (8)$$

$$\left(\frac{2\pi}{T}\right)^2 = \frac{2\pi g}{L} \tanh \frac{2\pi h}{L}, \qquad (9)$$

so that the hydrodynamic filtering effect $\Delta P/\Delta P_0$ can be computed as a function of depth and wave period. For instrument depths (on the bottom) of 40, 150, and 600 ft, the pressure fluctuations for wave periods of 4, 8, and 16 sec, respectively, are reduced to 10 per cent of their surface value ($\Delta P/\Delta P_0 = 0.10$).

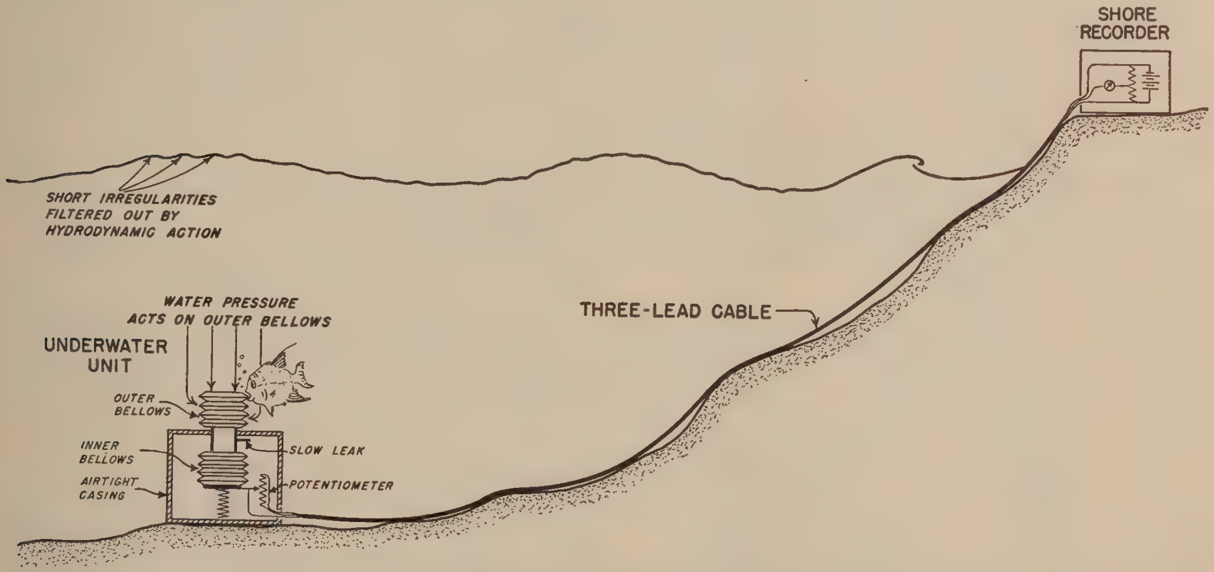

Fig. 4.—Recording mechanism. The pressure is transmitted through an outer bellows into a second bellows inside the instrument casing, so that the pressure of the air inside the two bellows always equals the pressure in the water outside. The air inside the bellows can pass through a slow leak into the instrument casing, and the *average* pressure inside the casing equals the *average* pressure in the water, that is, the hydrostatic pressure. The leak is so slow that the pressure inside the instrument does not change appreciably during one wave period, yet it permits pressure equalization related to tides. The total displacement of the inner bellows depends on the *difference* in pressure between the inside and the outside of the bellows and therefore measures the deviations of pressure (amplitude ΔP) from the hydrostatic mean.

Measurements by Seiwell [13] would indicate that equations (8) and (9) are in error by approximately 20 per cent.[6] Ewing and Press [4] have suggested that this discrepancy might be related to the nonrigidity of the sea bottom. Folsom [5] obtains about half this discrepancy in laboratory experiments employing metal wave tanks, thus indicating that the discrepancy might also be related to other factors.

Two methods for determining *wave direction* are being investigated. At the Department of Engineering, University of California, Berkeley, J. D. Isaacs has measured wave direction by means of a Rayleigh disk attached to the underwater unit. The orientation of this disk is recorded ashore by means of a Selsyn motor. In the case of a simple wave train the disk will align itself normal to the plane of orbital motion. In the case of an interference pattern the records are difficult to interpret. At the Scripps Institution, R. S. Arthur is investigating the determination of wave direction from a comparison of the phase relationships of records from two underwater instruments placed roughly parallel to shore. The development of a reliable method for measuring wave direction is an essential requirement in making use of wave records for tracking storms.

Interpretation of Records. In order to overcome the almost prohibitive labor involved in carrying out harmonic analysis by numerical computations, a very effective instrument for frequency analysis has been developed at the Admiralty Research Laboratory in Teddington, England [2]. Figure 5 shows a set of period analyses obtained by the methods discussed above.[7] The first indications of the storm on the wave record were some "low-frequency noises" at 1400, 14 March 1945. At that time visual observations at Pendeen revealed only the presence of 10-sec and 12-sec waves from another source; the long forerunners of the swell were too low to be visible.

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[6] Seiwell uses the deep-water formula $(2\pi/T)^2 = 2\pi g/L$ rather than equation (9) (see discussion by Ewing and Press [4]).

The band of gradually diminishing periods was the result of an intense storm which formed on 10 March off the coast of Cuba, 3000 miles from Pendeen, and traveled in a general northeast direction, passing west of the British Isles. Four representative weather maps are shown in Figs. 6–9. The positions indicated for the "fetches" were determined according to the rules developed for wave forecasting.[3] It should be noted that the fetch lengthened during the time interval between 1830, 11 March, and 1830, 12 March.

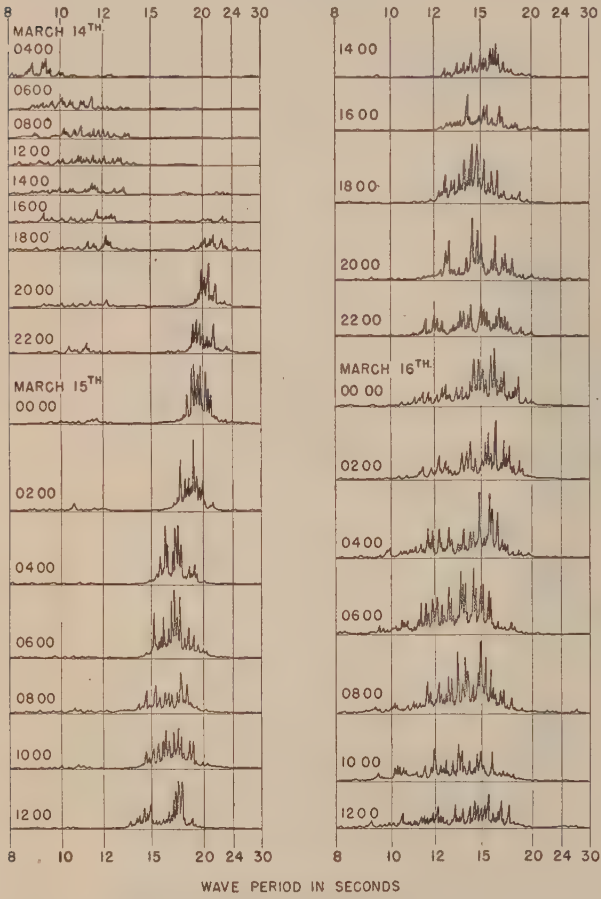

FIG. 5.—Spectrograms of waves recorded during 14–16 March 1945 at Pendeen, England [1]. Each spectrogram gives the distribution of energy among wave periods for a 20-minute record. The records were taken at 2-hourly intervals.

The spectrogram in Fig. 5 can be interpreted in terms of the classical wave theory, according to which component wave trains travel independently with the group velocity appropriate to their period:

$$V = \frac{gT}{4\pi} = \frac{x_w - x_s}{t_w - t_s}. \tag{10}$$

Here x_w and x_s represent the location of a point disturbance and the wave station, respectively; t_w and t_s the time of the disturbance and the time at which waves of period T arrived at the wave station. Equation (10) has a simple geometric interpretation on a time-distance diagram (Fig. 10): Rays through the point source represent the paths of wave periods, the value of each period being determined by the slope of the ray. The measurement of two periods, T_1 and T_2, arriving at times $t_{w,1}$ and $t_{w,2}$, suffices to determine distance and time of the source.

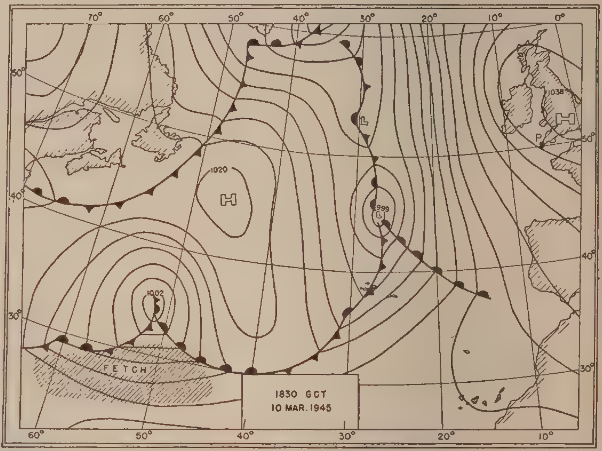

FIG. 6.—Surface weather map for 10 March 1945. Fronts are represented in the conventional manner, and isobars are labeled in millibars. Point *P* denotes the wave station at Pendeen, England. Figs. 6–9 show the passage across the Atlantic Ocean of the storm for which the wave spectrograms are shown in Fig. 5. (*From Munk* [9].)

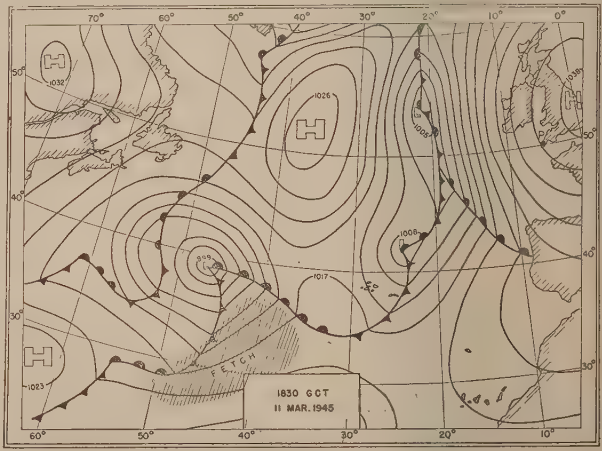

FIG. 7.—Surface weather map for 11 March 1945.

Figure 11 shows the *propagation diagram* used by Barber and Ursell [1]. For each spectrogram (Fig. 5) the maximum and minimum periods were determined, and lines of appropriate slope drawn. It is apparent from the figure that the foregoing interpretation of the wave observations is consistent with the meteorological observations. The author has found it convenient to use a graph [9, Fig. 5] with a special coordinate system on which periods from a single disturbance fall along a straight line. In this manner certain outstanding features on the spectrogram (such as the upper and lower limits) were used to determine the distance and time of the source region with which they are associated.

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[7] A different type of analysis based on the autocorrelation function has recently been applied to ocean waves by Seiwell and Wadsworth [14].

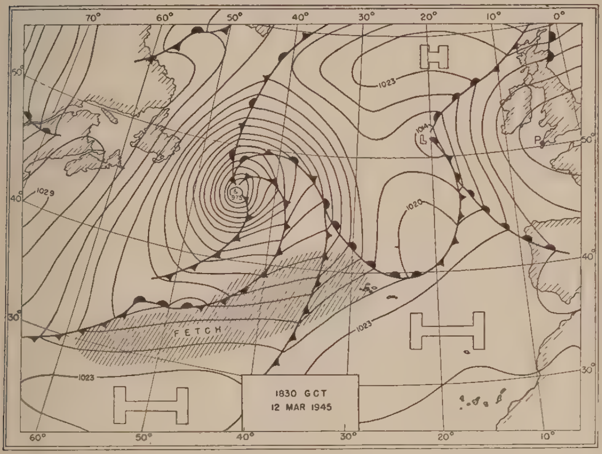

Fig. 8.—Surface weather map for 12 March 1945.

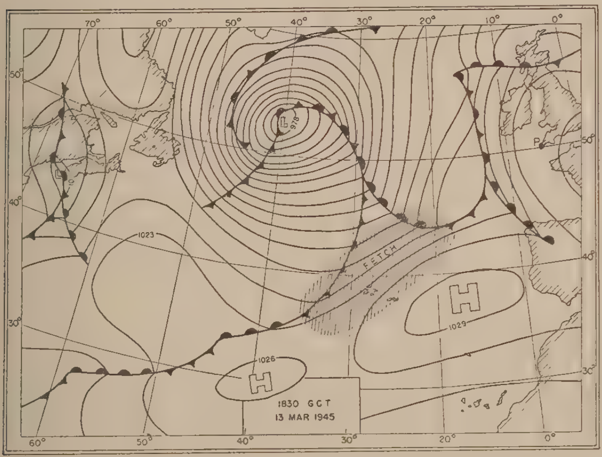

Fig. 9.—Surface weather map for 13 March 1945.

The information taken from the weather maps and the periods recorded at the wave station have been replotted in Fig. 12 to emphasize the similarity, with regard to both shape and width, between the storm path and the period band. The computed positions, designated by *A*, *B*, . . . *F*, agree fairly well with the information on the weather maps, especially if it is remembered that these "foci" were obtained from theory without the introduction of any arbitrary constants. The foci *A*, *B*, and *C* were computed from the lower limit of the period band and seem to correspond to the forward edge of the fetch; *D*, *E*, and *F* were computed from conspicuous features near the upper limit of the period band and give the approximate position of the rear edge of the fetch. It can be seen, however, that focus *A* in the upper part of Fig. 12 is located 500 miles

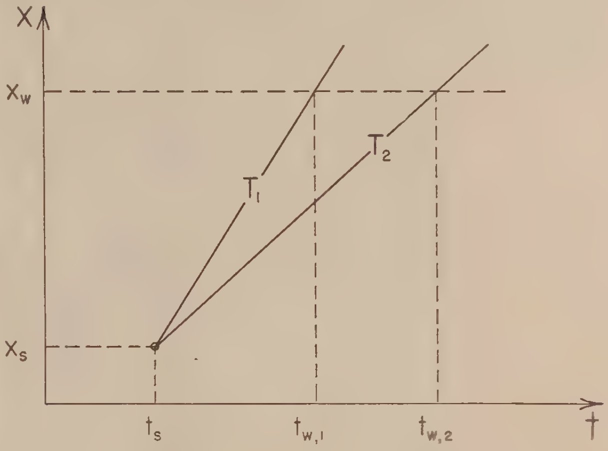

Fig. 10.—Schematic presentation of propagation of wave periods on a time-distance diagram. x_s and t_s represent the position and time of a point disturbance; x_w is the position of a wave-recording station, showing the arrival of waves of periods T_1 and T_2 at times $t_{w,1}$ and $t_{w,2}$, respectively.

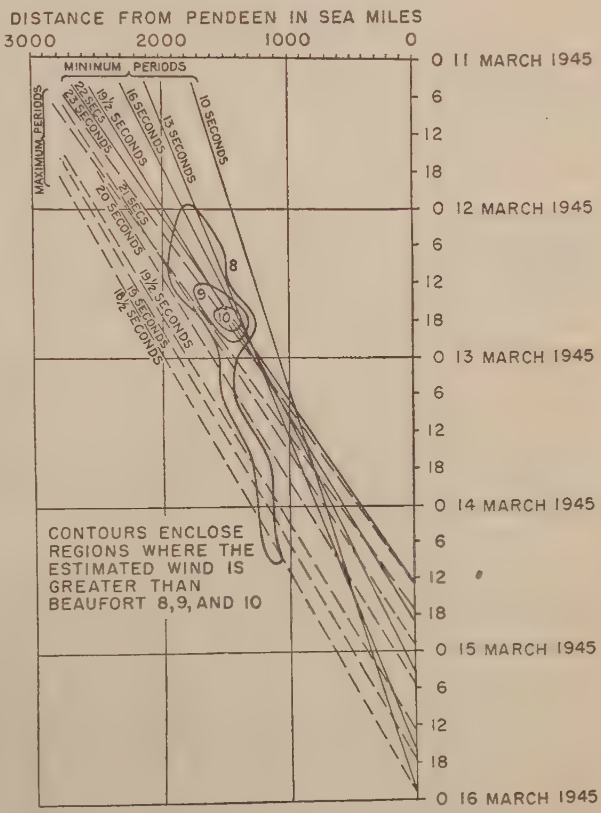

Fig. 11.—Propagation diagram for 11–16 March 1945, using winds estimated from the pressure distribution, flowing within 30° of a line of the recording station. (*From Barber and Ursell* [1].)

behind the storm front, and the other two foci about 200 miles behind the front. These discrepancies must be expected, since waves generated at the front itself could not gather sufficient energy to be perceptible at the wave station; furthermore, the distance between the point of wave origin and the storm front must be larger for the farthest disturbance, which is almost 3000 miles from Pendeen.

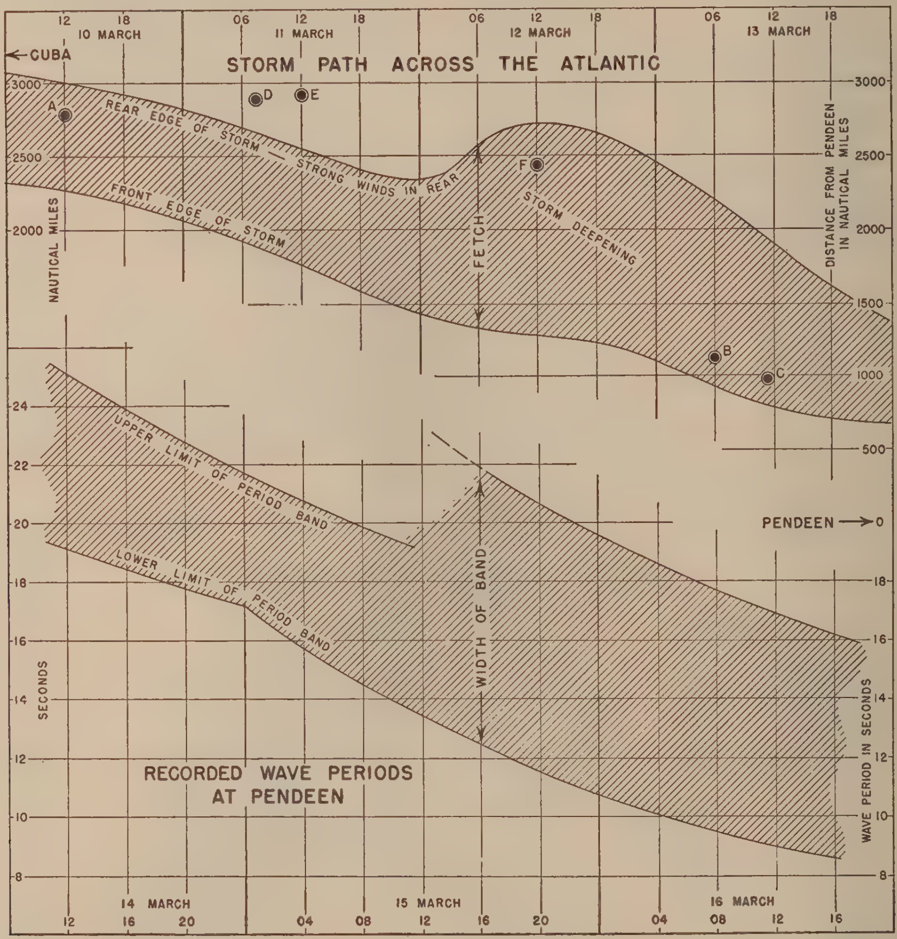

Fig. 12.—Comparison of storm path with period band. The shaded band in the upper part shows the movement of the storm system toward the wave station. The forward and rear edges of the storm were determined by 6-hourly weather maps, of which every fourth map is shown in Figs. 6–9. The computed storm positions (foci) are marked *A*, *B*, . . . *F*. The limits of the period band in the lower part were determined from the wave spectrograms shown in Fig. 5. (*From Munk* [9].)

Figure 13 illustrates the application of the method to a more complex meteorological situation. Two storm systems which existed simultaneously could be identified and traced separately. On 15 February 1945 the development of a cyclone started off the east coast of the United States. On 17 February the center of the cyclone had reached mid-Atlantic, and an unusually well-defined 1000-mile fetch in the warm sector was pointing directly toward the wave station. At the same time a new low-pressure area had just moved off the east coast of the United States and formed a second fetch immediately north of Bermuda (Fig. 13, upper right). As the first storm stagnated and veered northward toward Iceland, Pendeen came under the influence of the fetch in the cold sector, which remained at about the same distance from Pendeen. In the meantime the fetch in the warm sector of the second storm moved slowly eastward, and on 18 February this and the fetch remaining from the first storm appeared as a single generation area. By 19 February the first storm had undergone complete frontolysis. The only remaining fetch was that in the cold sector of the second storm, which was moving northward toward Iceland.

The spectrograms shown in Fig. 13 are more complicated than those in the preceding examples, and the interpretation is much more difficult. The first three foci fall in the first storm as it moved across the Atlantic. Foci *D* to *H* are associated with wave trains that were formed as the first storm veered northward and its fetch was joined with the fetch of the second storm. Only by that time had the main-period band moved sufficiently into the lower periods to permit identification of a wave train, *F*, from the distant second storm. Foci *J* to *N* originated from the joint fetch existing from

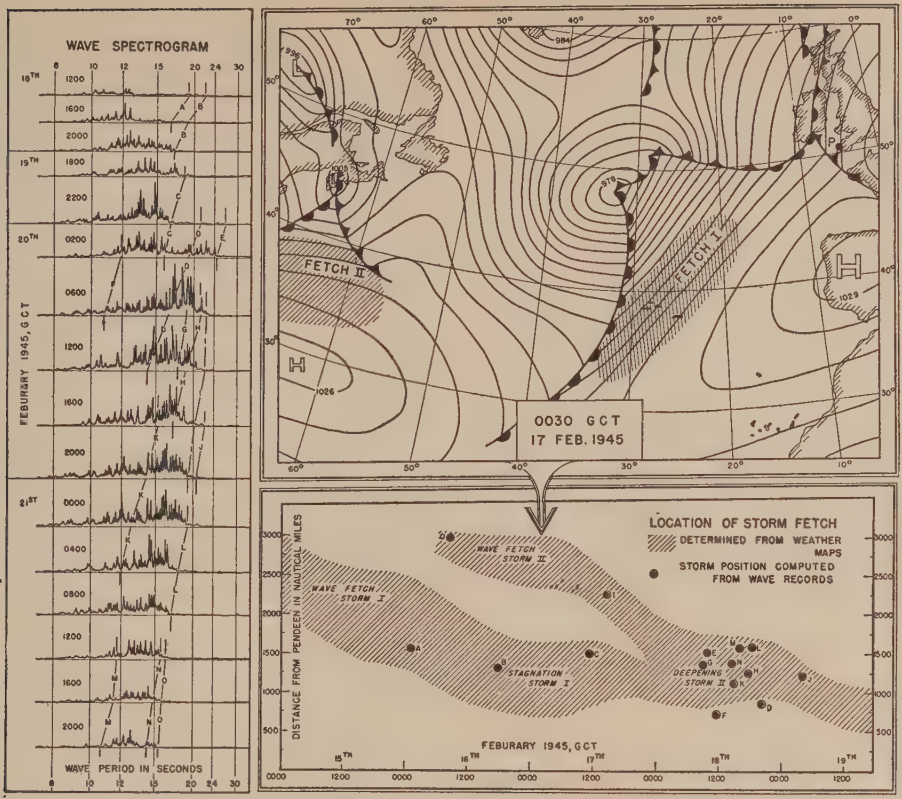
WAVE SPECTROGRAM
8
10
12
15
20
24
30
18TH
19TH
20TH
21ST
FEBURARY 1945, GCT
WAVE PERIOD IN SECONDS
FETCH I
FETCH II
H
L
1026
1029
978
984
0030 GCT
17 FEB. 1945
LOCATION OF STORM FETCH
DETERMINED FROM WEATHER MAPS
STORM POSITION COMPUTED FROM WAVE RECORDS
DISTANCE FROM PENDEEN IN NAUTICAL MILES
WAVE FETCH STORM II
WAVE FETCH STORM I
STAGNATION STORM I
DEEPENING STORM II
FEBURARY 1945, GCT
15TH
16TH
17TH
18TH
19TH

FIG. 13.—Application of storm-tracking method to wave records of 18–21 February 1945. The period spectrograms recorded at Pendeen are shown to the left. Significant features on adjoining records are connected by dashed lines, marked *A*, *B*, . . . *O*. The corresponding foci are shown by the circles in the diagram at the lower right, where the shaded band gives the path of the storm determined from weather maps. One of these weather maps is shown at the upper right. (*From Munk* [9].)

18 to 19 February, but focus *O* had its origin in the second storm system when it was still 3000 miles from the wave station.

Discussion. A considerable number of meteorological sequences have been studied by means of the Pendeen wave records, and in all instances the agreement between computations based on the wave records and the information on the weather maps was encouraging. In one instance, 26 June 1945, waves from a hurricane off the coast of Florida were faintly recognizable above the disturbance caused by a moderate local storm. To the author's knowledge, attempts based on wave records taken along the coasts of the United States have not been equally successful. This can be attributed at least partly to instrumental difficulties.

At one time the author had hoped that by shifting the range of maximum response of the instruments toward longer periods (by placing recording units of greater sensitivity in deeper water) it should be possible to record even longer forerunners, with periods, say, up to 60 sec, and correspondingly high velocities. Experience in England [1] does not support this expectation. Figure 14, based on thirteen well-substantiated storms, shows a correlation between maximum wind force of *distant* storms and the maximum recorded swell period. A possible explanation is contained in the forecasting theory [16] according to which waves gain energy from the wind only if the wave age (wave velocity/wind velocity) is less than 1.37. The dashed line in Fig. 14 corresponds to values of the wave age ranging from 1.26 to 2.26. The preliminary conclusion is that fore-runners with periods longer than 25 sec, or perhaps 30 sec, are so low compared to other types of wave motion in that period range [10] that they would be associated with an unfavorable signal-to-noise ratio. Accordingly, the highest group velocities which one may

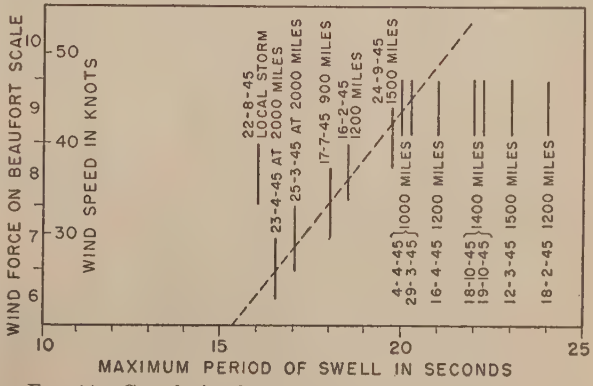

FIG. 14.—Correlation between the maximum wind strength and the maximum period of swell generated for thirteen storms. (*From Barber and Ursell* [1].)

hope for are of the order of 1000 nautical miles per day. Not until many more situations have been analyzed will an evaluation of the usefulness of the method be possible. The results so far obtained demonstrate the feasibility of locating and tracking storms at distances exceeding 3000 miles and of making rough estimates regarding the size and character of these storms.

The Storm Surge Method

The preceding discussion has indicated that the swell spectrum, visible or invisible, is limited by the maximum velocities of the winds in a storm area. This conclusion is in accord with the hypothesis that swell was originally caused by the normal and tangential stresses applied by the wind to the sea surface, but it does not preclude the existence of other types of waves from storm areas of much longer period than those of the swell. To explore this possibility an instrument [11] has been built which is sensitive to waves whose periods lie between those of the swell and tides. It is essentially a modified tide gauge, and the filtering of the swell and tides is accomplished by means of capillaries and air volumes. The instrument does not require the expensive and troublesome underwater cable and is therefore simpler and much less expensive than the underwater pressure recorder described in the preceding section. One such unit has been installed at the end of the Scripps Institution pier at La Jolla, California; a second unit has recently been installed in Hawaii.

Table II. Data for Five Severe Storms off the California Coast

Date (1948)	Earliest storm surges			Maximum storm surges			Maximum swell			
	Date and time	H (ft)	T (min)	Date and time	H (ft)	T (min)	Date and time	H (ft)	T (sec)	Warning period (hr)
Feb. 9–10	9:0500	.04	14	9:2230	.12	15.5	10:1500	6	8	34
Feb. 21–23	21:1800	.06	15	22:1100	.15	15.5	23:0400	8	9	34
Feb. 27–29	27:1400	.06	12	28:0600	.12	14	29:1200	4.5	11	46
Mar. 30–31	30:1000	.10	20	30:1600	.14	12	31:1200	7.5	8	26
Apr. 22–24	22:0800	.08	18	22:2200	.09	13	24:0700	9.5	8.5	47
									Mean:	37

During the spring of 1948 five severe storms passed off the coast of California. In each of the five cases, waves of periods of approximately 15 min (storm surges) were received from 24 to 36 hours prior to the arrival of the heaviest surf and the strongest winds.

Some of the data are summarized in Table II, giving the height H and period T of the storm surges, and also of the swell as it was recorded on the underwater recorder at a depth of 40 ft. The mean height of the storm surges was only 1 in. and it is quite clear that these waves could be detected only by special instruments. According to Table II the earliest arrival of the storm surges preceded the heavy swell by one and one-half days on the average.

It must be emphasized that the study of these storm surges is in a preliminary stage, and that the manner in which they are generated is not at all understood. Should it be possible to use storm surges in locating storms at sea, they would have the advantage of relatively high speed, $\sqrt{gh}$ in water of depth h, or 10,000 nautical miles per day in mid-ocean. It is hoped, therefore, that they may eventually provide a tool to the synoptic meteorologist.

Discussion and Conclusions

The relative merits of the three methods involving the propagation of ocean surface waves are summarized below. We shall also point out some of the disadvantages and advantages of these methods as compared to methods involving the propagation of sound waves through the sea bottom (microseisms) and electromagnetic waves through the atmosphere (radar and spherics).

Instrumentation. The height-period (HT) method requires no special instrumentation. The frequency-spectrum analysis (FA) method requires an underwater recording unit connected by a cable to a shore recorder. Along rocky coasts and coral reefs the chafing of the cable may create quite a serious problem and the use of expensive and unwieldy armored cable may be required. A frequency analyzer must be available at each location if the method is to be used synoptically. The storm surge (SS) method involves a much simpler installation, provided a pier or breakwater is available for securing the instrument.

Storm Location. The bearing and distance of a storm can be located by the HT and FA methods from a single station. In the case of the HT method a visual estimate of wave direction should suffice in view of the uncertainties regarding the determination of distance. The theory underlying the method is insecure, and it is also necessary to make assumptions regarding the duration of the storm. Furthermore, an estimate of deep-water wave height from shore observations may be subject to considerable error. The HT method has the advantage that it permits some estimate of the storm location from a single set of simple observations.

The FA method, on the other hand, depends upon the determination of a *shift* in the frequency spectrum and requires therefore (intermittent) observations extending over a minimum period of perhaps six hours. The determination of distance is based on sound physical theory, and furthermore does not involve the determination of wave height. In the determination of wave height the response characteristics of the instrument enter as an important factor, and it may be necessary to take into account, by means of specially constructed "refraction diagrams" [7, 12], the effect of bottom topography and of the configuration of the coastlines. Wave periods, on the other hand, are relatively easy to ascertain from wave records and are not subject to the complex changes in wave pattern that occur as waves come into shallow water. Determination of wave direction by means of a Rayleigh disk or a two-unit wave station are being investigated.

It is not likely that the SS method will make it possible to compute the storm distance from records at a single station. The distance determination for the FA method depends upon the high dispersiveness of ocean swell, and storm surges are almost nondispersive. In view of the great length of storm surges they will also be subject to considerable refraction. The principal hope lies in the determination of the arrival time of identical phases at two or three stations, and the location of storms from special charts based on the propagation at $\sqrt{gh}$ velocity.

Range. It is estimated that the HT method can be used to distances up to 3000 nautical miles, the FA method to distances exceeding 3000 miles. The range of the SS method is not known. The values given above are in excess of those that have been obtained by seismic and electromagnetic methods.

Group Velocity. The group velocities applicable for the HT, FA, and SS methods are of the order of 400, 900, and 10,000 nautical miles per day respectively. The relatively long interval between the time the waves are generated and the time they are recorded at the wave station is a disadvantage in the application of the HT and FA methods. Their practical use will, therefore, be largely to verify or modify the interpretation already made on the basis of meteorological information. In the case of compact meteorological disturbances, such as young hurricanes, these waves may well provide the first clue as to the existence of the storms. The methods should be particularly useful over the southern oceans [3] and for other regions where the network of observing stations is widely spaced. The group velocity of the storm surges, although slow compared to the seismic and electromagnetic waves, is sufficiently large to permit synoptic application.

Storm Intensity. The HT method gives an estimate of the storm intensity. In the case of the FA method an estimate of wind speeds from the maximum recorded period is suggested by Fig. 14. It is also hoped that studies dealing with the propagation of *energy* by the forerunners will lead to an interpretation of the spectrogram *ordinate*, which has received no attention so far but must be related to the storm intensity. The relationship between storm intensity and storm surges has not been studied.

Other Storm Characteristics. The application of the methods employing ocean surface waves is further enhanced by the possibility of determining not only the location and intensity of the storm, but also its size, type, acceleration, and other characteristics. In view of the close "coupling" between the wind pattern and the sea surface waves one might expect a better chance for success by the methods described in this report than by those based on seismic and electromagnetic waves.[8]

Desirable Future Studies. With regard to the HT method the research requirements coincide with those pertaining to the problem of forecasting ocean waves and are discussed in another paper.[3] Of particular importance is a better understanding of the decay of swell traveling through an area of calm or cross winds. In this connection it is planned to establish a wave recorder in the equatorial Pacific, possibly on the Marquesas Islands. These islands lie 2400 miles and about 6 days "up-swell" from California, and a comparison of wave records obtained there with those at Oceanside, California, would give information concerning the attenuation of swell over large distances. It is hoped that these studies may help to bring about, on a scientific basis, a revival of the ancient art of judging weather from the appearance of the sea surface.

The FA method appears to have reached a stage of development where it will be possible to work with records from a network of stations, rather than from a single station. We may expect marked progress as a consequence. Our present experience is almost entirely confined to stations in the eastern Atlantic *toward* which the storms were moving.[9] Development and standardization of suitable recording and analyzing equipment is urgently needed. The determination of wave direction is an essential requirement in making use of wave records for tracking storms.

The SS method is at such an early stage of development that further work along instrumental and theoretical lines is required before it is possible to make any definite recommendations. An improved instrument has been installed at the end of the Scripps Institution Pier, in La Jolla, California, and similar units will be installed during 1950 at Oceanside, California, 30 miles north of La Jolla (for direction determination) and in Hawaii. By means of this network of long-period-wave stations it is hoped that research on the generation and propagation of storm surges can be vigorously pushed.

In conclusion it must be emphasized that it would be most unfortunate if study were to be limited to the three methods with which we have been chiefly concerned here. A systematic exploration of the spectrum of ocean waves is likely to lead to surprising new developments. In this connection it should be remembered that the sea surface wave pattern provides a complete picture, though a distorted one, of the entire wind distribution over the ocean, and our interpretation of this picture should improve with the advance of instruments, of theoretical studies, and of empirical experience.

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[8] Recent evidence [3] indicates that some of the microseismic activity is caused by the interference pattern of the surface waves in the storm area. Apparently a second-order effect inherent in such a pattern is associated with pressure fluctuations which do not disappear at great depth.

[9] Lt. R. L. Miller, USAF, has successfully applied the method to a storm over the Bering Sea, using wave records taken at Guam, located to the *rear* of the moving storm (*Scripps Institution Wave Report No. 90*, unpublished).

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THE USE AND ACCURACY OF THE EMERY SETTLING TUBE FOR SAND ANALYSIS

TECHNICAL MEMORANDUM NO. 23
BEACH EROSION BOARD
CORPS OF ENGINEERS

JULY 1951

Contribution from the Scripps Institution of Oceanography, New Series, No. 513

FOREWORD

This paper was prepared by Messrs. D. M. Poole, W. S. Butcher and R. L. Fisher of the Scripps Institution of Oceanography and represents in part the results of research performed at that Institution for the Beach Erosion Board. An early version of this report, since modified, first appeared in limited issue in April 1950 as Submarine Geology Report No. 9 of the Scripps Institution of Oceanography, University of California. It is believed that the findings of the investigations are of sufficient value to merit publication for wider distribution at this time.

The opinions and conclusions expressed by the authors are not necessarily those of the Board.

The authority for publication of this report was granted by an Act for the improvement and protection of beaches along the shores of the United States, Public Law No. 166, Seventy-ninth Congress, approved July 31, 1945.

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THE USE AND ACCURACY OF THE EMERY SETTLING TUBE FOR SAND ANALYSIS

by

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R. L. Fisher

ABSTRACT

The accuracy of the Emery Settling Tube for the analysis of sand particles has been investigated. As pointed out by Emery, this method is more rapid than dry sieving and gives equivalent, or settling, diameters rather than geometric diameters. It is felt that a more exact knowledge of the errors and limitations of the method would be valuable.

It was found that the settling tube analyses for material between 0.062 mm. and 1.0 mm. had a reproducibility or coefficient of variation of the median diameter ranging from 0.6 - 2.0%, reproducibility being poorest for the coarser grades. Over the same range the coefficient of variation for sieving was 0.4 - 0.7%. For most beach sands the accuracy of the two methods is very nearly the same. The errors occurring during splitting of the sample to the proper size were investigated by several procedures, but the results were not conclusive. The maximum splitting error was 3.6%. The effect of material finer than 0.062 mm. in the sample was investigated and it was found that no significant difference was produced where the fine material was 10% or less of the total. The effect of material coarser than 1.0 mm. in the sample was also investigated and it was determined that all coarse material should be removed before the settling tube analysis is made.

A recommended procedure for making such an analysis is included.

Introduction

Emery (1938) described an instrument for the rapid and accurate mechanical analysis of material of sand size. In the original paper there was not sufficient information to indicate the accuracy of the method for procedure to be followed in making an analysis. This paper further confirms the reproducibility of the results obtained from the settling tube, the close correlation with sieve analysis, and gives a detailed recommended procedure. The equivalent diameters obtained by this method would appear to be more indicative of erosional and depositional features than those obtained by sieving, particularly where there is a high percentage of micaceous or platy material. The time saved by this method over dry-sieving is of great advantage where there are numerous samples to be analyzed. On one occasion 57 well-sorted, medium-fine grained sand samples were run down the tube in 3 hours and 15 minutes.

Essentially the Emery Settling Tube is a glass tube of 21 mm. inside diameter and 164 cm. length. At the bottom the tube narrows to 7 mm. inside diameter and is closed with a stopcock. The narrow portion of the tube above the stopcock is engraved with milliliter divisions on which to read the cumulative heights of sediment. Emery (1938) gives a figure of the settling tube used by him; the one in present use is similar.

The aim of the investigation was to determine the reproducibility of the method, to determine the splitting errors encountered in preparing the sample, to evaluate the effects of particles coarser than 1.0 mm. and finer than 0.062 mm. in diameter, to evaluate the effect of the weight of the sample used, and to compare the settling tube analysis with that obtained using standard sieves. These effects are discussed separately in the following sections. A recommended procedure to be followed in making an analysis by this method is given at the end of the paper and is based on experience gained in using the settling tube and the results of this investigation.

Method of Investigation

The Emery Settling Tube was used, in all the tests, in the manner outlined in the section entitled "Procedure". Briefly, this consists of splitting the bulk sample to 3.5 - 4.5 grams, introducing this small sample into the Emery Settling Tube, and reading cumulative heights at times corresponding to the settling time for a given sized material in distilled water at the observation temperature (see Sample Data Sheet, Figure 1). For purposes of comparison, a sieve analysis was made in certain cases using the Tyler Standard Screen Series, based on the $\sqrt{2}$ grade scale. The shaking time for the sieve analysis on a mechanical shaker was 10 minutes.

Median diameters and statistical properties determined in this study are reported in the phi scale proposed by Krumbein (1934b), where $\phi = \log_2 \text{mm}$. The measure of sorting used in this study is the phi standard deviation, $\sigma\phi$, based on the 16th and 84th percentile diameters of the cumulative frequency curve. (Otto, 1939). This parameter is chosen because it approximates the standard deviation of mathematical statistics. The cumulative volume percentage for each grade of the Emery Settling Tube and the cumulative weight percentage for each grade of the sieve analysis are plotted on arithmetic probability paper. From such plots the phi median diameter and phi standard deviation were noted. From these data the following properties were computed:

(a) Value of the given characteristic for each sample, M.

(b) Mean of that characteristic for the suite of samples, m.

(c) The standard deviation of the distribution of n samples $\sigma = \sqrt{\frac{\Sigma (m-M)^2}{n-1}}$ or the degrees of freedom being used in the denominator because of the small number of samples concerned (small sample theory), Snedecor (1946).

(d) The coefficient of variation (relative standard deviation), C, defined by $C = \frac{\sigma}{m}$.

For comparison between different tests it is necessary to have the error expressed nondimensionally. Such a coefficient of variation or relative standard deviation was obtained by dividing the standard deviation by the mean of the value of the property concerned, and multiplying the quotient by 100 to obtain a percentage.

As shown by Krumbein (1934a), the total error may be separated into any number of independent component errors, the relationship being $E=\sqrt{e_1^2+e_2^2+e_3^2+\cdots e_n^2}$. Krumbein used total error to mean "total standard deviation" or, equally well, "total probable error". In this paper, however, the total error is taken to mean total coefficient of variation, but the same relation holds. Since the coefficients of variation are expressed in percent (see above), they are non-dimensional and apply to any test. In this paper the total error of the analysis, $E=\sqrt{e_1^2+e_2^2}$ where e_1 is the settling tube error and e_2 is the splitting error.

Reproducibility

Settling Tube Error: If the same sample is run through the settling tube a number of times, the variation of results is due to the errors in running the sample through the tube, observational errors, and errors in timing. These may be considered as the error of the settling tube itself or of the method, since splitting and weight-of-sample errors do not enter. In order to test the reproducibility of the settling tube, several series of runs were made, each series consisting of repeated runs of one split of a given sample. After each run, the sample from the tube was collected in a beaker and reintroduced into the tube. The median diameters ranged from 2.95ϕ (0.130 mm.) to 0.59ϕ (0.66 mm). For comparison, sieve analyses were run on some of these samples. The results of the settling tube and sieve analyses are summarized in Table I.

TABLE I

			Phi Median Diameter, Mdϕ			Phi Standard Deviation. $\sigma\phi$	
Sand Type and Locality	Type of Analysis	Number of runs n	Mean m	Standard Deviation σ	% Coef. of Variation C	Standard Deviation σ	% Coef. of Variation C
Yuma dune sand (Fig 2)	Settling tube	10	2.95ϕ	0.0138ϕ	0.5%	0.015ϕ	3.2%
	Sieve	6	2.89	0.0118	0.4	0.0118	2.7
St. Peter Sandstone	Settling tube	16	0.59	0.0234	4.0	0.0146	4.9
	Settling tube tap water	16	0.58	0.0294	5.1	0.01	3.8
Gold Beach, Oregon, sand	Settling tube	16	0.90	0.0159	1.8	0.0269	5.1
	Sieve	8	0.78	0.0037	0.5	0.0066	2.2
San Nicolas Is. beach sand I.	Settling tube	16	2.02	0.0157	0.8	0.0107	2.0
	Sieve	8	1.88	0.0076	0.4	0.0181	3.0
San Nicolas Is. beach sand II	Settling tube	14	1.53	0.018	1.2	0.0213	3.8
	Sieve	8	1.39	0.0093	0.7	0.0066	1.4
Artificial bimodal	Settling tube	16	1.53	0.0163	1.1	0.0366	10.6

Several conclusions seem warranted by these data:

a. In nearly every case, the sorting or phi standard deviation determination is less reproducible than the median. This is due in part to the fact that the mean value of the standard deviation, the denominator in the coefficient of variation expression, is a small number, much less than one for these relatively well-sorted sands.

b. The equivalent diameter by sieving is greater (coarser) than that obtained by settling tube analysis.

c. Settling tube accuracy (Figure 3) falls off rapidly for material coarser than about 1.0φ (0.5 mm.). The use of distilled water is not essential in the analysis of such coarse material, providing the tap water is free of sediment.

A comparison of the reproducibility of the settling tube and sieve analyses is shown in Figure 3. The upper curves are based on the standard deviation of the phi median diameter, as expressed in column 5 of Table I. Standard deviation, σ, is a measure of the spread of a distribution. Therefore reproducibility or accuracy of a property such as median diameter is inversely proportional to the standard deviation of a series of measurements of the property. The standard deviations of the median diameters obtained from the settling tube runs decrease with decreasing grain size (increasing phi). This decrease in deviation is mainly due to the greater accuracy in reading the height of a column of sediment which is settling out slowly, as compared to the material settling and accumulation for coarser material. In the case of coarser material settling and accumulation occur so rapidly that exact timing is critical. Sieve analyses show a slight increase in deviation with decreasing grain size. This increase may be reduced by shaking the finer samples for greater lengths of time, followed by a very thorough cleaning of the sieves.

The lower pair of curves in Figure 3 show the reproducibility of median diameter with grain size in terms of the non-dimensional coefficient of variation, C. The coefficient of variation is the quotient $\frac{\sigma}{m}$ and is obtained from column 6 of Table I. Since the divisor, m, approaches zero the trend for the settling tube discussed above is greatly accentuated. For coarse sand the phi median is less than one; for fine sand, it is about three. The coefficient of variation of the analysis is thus much smaller for fine sediment. This coefficient for sieve analysis is much more constant over the sand range. Both settling tube and sieve analyses approach a coefficient of variation of about 0.5% for fine sand. Although the curve for the settling tube indicates progressive increase in accuracy with decrease in grain size, the behavior of particles finer than 4.0φ has not been accurately determined. The smoothed curves may be accepted as expressing the reproducibility of analysis over the range of the Emery Settling Tube, although in a strict sense they apply only to one particular tube and set of observers.

An artificial distribution was obtained by combining a medium-grained sand and a micaceous fine-grained sand yielding a bimodal sample with a median of 1.53φ (0.34 mm.). One split was run down the tube 16 times; the median diameter was found to have a coefficient of variation of only 1.1%, but the Standard Deviation was extremely variable (coefficient of variation 10.6%) due to the samples bimodal nature, the fine mode becomming important above the 80 percentile of the cumulative curve. This sample may be compared with the unimodal sample of the same median diameter discussed above. While the coefficients of variation of the median diameters are nearly identical, the variations in sorting differ greatly. Therefore, when it is desired that the size distribution of each mode be obtained accurately, the approximate node between the modes of a preliminary sample may be computed and another portion of that sample passed through a sieve mesh of the nodal diameter. The two portions thus obtained may then be run down the tube and computed separately.

Splitting Error: In running a sample split in different portions, the splitting error will be given by extracting the square root of the difference of the squares of the total error and settling tube error: $e_2=\sqrt{E^2-e_1^2}$. Two samples of sand from the La Jolla area were used in this study: a composite made up of fractions from Cove Beach (Md 0.52φ, 0.70 mm.), Windansea Beach (Md 1.52φ, 0.35 mm.), and Scripps Beach (Md 2.55φ, 0.17 mm.); and a sand sample collected in shallow water from La Jolla Bay (Md 3.30φ, 0.10 mm.).

Eight splits were taken from the coarse composite sample (Md 1.33φ) by combining alternate quarters as shown in Figure 4, and eight splits from the same sample without combining. The splitting error in the first case (combined) was 1.8%, and in the second case 1.2%. Further tests with 32 combined and 30 non-combined slightly finer sized samples (not shown) gave splitting errors of 3.6% and 2.8% respectively. It is felt that the homogeneity of most sand and the time saved by the less complicated method of splitting obviate the necessity for the use of the procedure of combining alternate quarters.

Analyses of 12 splits of a fine sample (Md 3.30φ) indicate a probable coefficient of variation of splitting error of 0.2%. The low value for splitting error in this case is due to the fact that this fine sand was more homogeneous than the coarser artificial composite discussed above.

Effect of Sample Weight: It was thought that some significant error might be introduced in the settling tube analysis if the weight of the material were not the same in each case. The error might come from the increase in density of the medium and from the greater tendency to advection currents with increased material. From Owen's (1911) data, it can be estimated that 5 grams of material in the 515 grams of water in the settling tube will affect the settling time by about 2.5% due to increase in the density of the medium, if the sand is considered to be in solution. As the sand is obviously not in solution, the error introduced must be considerably reduced and probably can be neglected. Calculations based on the formulas of Rubey (1933) indicate the same order of magnitude for the error introduced by increase of density of the medium. It is of advantage to have the sample as large as possible within the capacity of the settling tube, because a large sample gives a greater change in cumulative height for a given volume percentage of the total sample. Most of the error introduced should be due to advection current rather than to increase in density.

Four splits of a fine-grained sand (Md 3.02ø) were run (Figure 5), the splits having weights of 2, 3, 4 and 5 grams. The coefficient of variation of the median diameter was 0.6%. Since for such material the tube error was 0.5% these data suggest that there is no appreciable effect caused by difference in weight of the samples used.

Influence of Particles Coarser Than 0.0ø (1 mm.)

Two analyses of the same split of a beach sand were made in order to determine the effect of particles coarser than 0.0ø (1 mm.) on the settling tube determination of grain size distribution. The first settling tube analysis was made with the total split, which included 16% of material coarser than 0.0ø. The analysis was then repeated after the material coarser than 0.0ø had been removed by sieving. Cumulative curves of the two analyses, plotted on arithmetic probability paper, are shown in Figure 6. To make the curves strickly similar, the weight percentage coarser than 0.0ø has been added (at the 0.0ø grade) to the sample having the coarser material removed.

The differences in the cumulative curves from these two settling tube analyses result from several causes, the relative importance of which are difficult to evaluate. First the 8% difference in weight percentage at the 0.0ø grade is due in part to the fact that equivalent diameter (from the settling tube) and geometric diameter (from sieving) generally are not the same. Secondly, the median diameter for the case in which the entire sample is analyzed by settling tube is larger than that for the composite settling tube-sieve analysis. Part of this difference may be attributed to the carrying down of finer particles with the coarse material. However, if this process were quantitatively important, the settling tube curve should be very steep in the fine grade classes (little fine material recorded) rather than crossing the sieve-settling tube curve. Finally, this discussion is based on only two runs of one sample. Losses may have occurred in handling the sample, especially in the finer size grades. Further work is necessary to settle this point.

It is suggested that particles coarser than 0.0ø should be sieved out before attempting a settling tube analysis. A particularly cogent reason for sieving out even small fractions of coarse material is that such grains are likely to clog the narrow part of the settling tube, resulting in voids in the accumulated sediment column.

Influence of Particles Finer Than 4.0φ (0.062 mm.)

In evaluating the effects of material finer than 4.0φ in the settling tube analysis two effects must be taken into account. First, there are the inaccuracies present when both settling tube and pipette procedure are used in getting the size distribution of the sample. Secondly, fine material may be carried down by coarser grains in the settling tube analyses.

The pipette-settling tube effect may be illustrated by two hypothetical examples. Assume in each case a perfect separation by wet sieving at 4.0φ (0.06 mm.) perfect settling tube and pipette analyses for the respective portions of the sample, and a minimum of 10 grams for the pipette analysis.

Case I. 10% of the sample is finer than 4.0φ. The total sample must then be 100 grams (90 grams coarser than 4.0φ). For the settling tube this 90 grams must be split down to 4 grams requiring 6 splits and one recombination

(90-45-22½-11¼-5 5/8- 2 13/16- 1 13/32 + 2 13/16 = 4^+ grams).

Case II. 50% of the sample finer than 4.0φ. The total sample must then be 20 grams. The 10 gram portion coarser than 4.0φ may be reduced to about 4 grams in 3 splits and one recombination (10-5-2½-1¼ + 2½ = 4^- grams).

The additional operations particularly in Case I, probably introduce more error than if a portion of the total sample were analyzed by settling tube alone, since the above assumptions do not hold. The pipette-settling tube error is relatively greater in the case in which only a small amount of fine material is present. Furthermore, for unimodal samples the progressive finer grained classes contain a decreasing proportion of the sample. The effect of these small portions of fine material on the settling tube analysis is not great, even though their settling behavior differs somewhat from that of the coarser grains for which the settling tube was designed. Beach sands seldom contain much material finer than 4.0φ; therefore the settling times on the data sheets (Figure 1) have been extrapolated to 5.0φ (0.031 mm.).

The second effect is illustrated by Figure 7a and 7b. From one split of each sample material finer than 4.0φ was removed by wet sieving through a 0.062 mm. sieve. The samples in which the fines were not removed showed a coarser median grain size, indicating some of the fines were carried down by the coarse grains.

It is suggested that if material finer than 4.0φ in beach sand samples comprises about 10% or less of the total the entire analysis may be carried out with the settling tube. If fine material makes up more than about 10%, the sample may be passed through a 0.062 mm. sieve (4.0ø) the weight of fine material determined, its cumulative percent computed and this value added to complete the settling tube cumulative curve. In such a case it may be necessary to analyze the fine portion by the pipette method.

Procedure

The preparation of samples for analysis is discussed at length in Krumbein and Pettijohn (1938). The only procedures considered in this paper are the preparation of samples for analysis by means of the settling tube, and the method for running the samples through the tube.

Splitting the Sample: The sample after disaggregation is first passed through a 1mm. sieve to remove all particles coarser than 0.0ø. The percent by weight of the sample coarser than 0.0ø can then be calculated. If there is more than 10% material finer than 4.0ø in the sample, it should be removed by wet sieving through a 0.062 mm. (4.0ø) sieve. Then the per cent by weight of the sample finer than 4.0ø can be determined.

The sample is next split to a weight of approximately 3.5 - 4.5 grams for the settling tube analysis. This amount is about 2/3 - 3/4 of the capacity of a 1 dram, screw cap vial. The split sample may be conveniently stored in these vials until ready for analysis. A Jones type sample splitter was used to split the sample down to a weight of about 20 - 25 grams. The "Otto Microsplit" was used to split the sample further to the correct weight, or volume, for analysis (see above) by the settling tube. This change of splitters is merely a matter of convenience in handling the sample. Tests showed that the type of splitter used introduced no appreciable error in the analysis.

Method of Introducing Sample Into Tube: The method has been somewhat modified from that recommended by Emery (1938). A 50 ml. conical centrifuge tube (2.75 x 13.5 cm.) with its bottom cut off is used as an introducing tube. The bottom of the tube is closed by the thumb, the sand poured in and distilled water added by means of a wash bottle so as to remove the grains sticking to the sides of the introducing tube and to cover the sand about 3/4 of an inch. The sand is stirred thoroughly until no bubbles remain, and any particles floating on the surface can be made to sink by touching them with a wooden pencil. The sand can then be released into the tube. The tube should not be filled completely but to within 2.5 cm. of the top, so on adding the sample the tube will be completely filled. The tube should be of such a length that the distance of fall will be 164 cm. Care must be taken when introducing very fine sand that large density currents do not form. This may be accomplished by slightly tilting the introducing tube and allowing the sand to slide into the settling tube slowly. Tapping the upper part of the tube will help break up any density currents that form.

Several runs were made with very fine sand samples using disaggregating agents, sodium oxalate ($Na_2C_2O_4$) and sodium hexametaphosphate ($(NaPO_3)_6$), to wet the sand before introduction into the tube. The results were not significantly different from splits of the same samples which were wet with distilled water.

It was noted at times that the distilled water added to the tube contained fine bubbles. This bubble formation occurred when the distilled water supply was low enough to cause somewhat intermittent flow. Flocculation, by adsorption to the bubbles, occurs when the bubbles are quite small and numerous. Since such adsorption makes the analysis erroneous, it is advisable that no runs be made while such bubbles exist.

The temperature of the distilled water is measured by running the water from the outlet through a bottle containing a thermometer and then into the settling tube. At present, the water is led in and out through two holes in a cork fitting a small wide-mouthed bottle. The thermometer is held in a third hole so that its bulb is bathed by the flowing water.

Reading the Height of Sand: The stopcock stem, graduated in milliliters, is not tapped as recommended by Emery (1938). Compaction was seldom observed in the sand column if the sand particles greater than 0.0ϕ were removed, but with coarse sands some slumping may occur. The inaccuracies in reading the sand height due to the rapidly changing interface, plus the error due to slumping, indicate that the settling tube should not be used in analyzing samples containing an appreciable amount of coarse sand.

Summary and Conclusions

The time saved by making mechanical analyses of sand by means of the settling tube contrasted to sieving has already been printed out by Emery (1938). The present study further shows that:

1. Median diameters determined by means of the settling tube are reproducible to within less than 1% for medium to fine (very fine) grained sands in which mica makes up only a small fraction of the sample. Trends, based on scattered samples, showing differences of more than 1% are probably real, over this size range. Accuracy falls off rapidly for coarser material.

2. The standard deviation or sorting determination is less reproducible; that is, it generally has a larger coefficient of variation. This is due in part to the fact that the mean value of the standard deviation, the denominator in the coefficient of

variation expression, is a small number, much less than one for those relatively well-sorted sands. Variations in sorting of greater than 4-5% between two unimodal samples are probably real and significant.

3. For coarse sand the sieve method is much more accurate than the settling tube method. For fine sand the difference in accuracy is probably balanced by field and splitting errors, and by the time saved in the settling tube method. It must be kept in ming that settling tube analyses yield equivalent diameters, rather than the geometric diameters obtained by sieving. These two measures differ most when platy material or minerals other than quartz or the feldspars make up an appreciable portion of the sample. In the erosion, transportation and deposition of sediments equivalent diameters are probably more significant than are geometric diameters.

4. No very definite value can be assigned the error introduced in splitting the sample to the correct size. It ranged from 0.2% for homogeneous fine sand to 3.6% for a coarser composite sand. No gain in accuracy was observed when the method of combining alternate quarters was employed.

Acknowledgments

Acknowledgment is made to Mr. D. L. Inman for his constructive suggestions during the course of the investigation and his critical reading of the manuscript. Miss Ruth Young assisted in the collection of data. Mr. D. B. Sayner is to be thanked for drafting the several diagrams.

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Mechanical Analysis Sheet No. 1 (Revised May 1951) Sample Date No. ______________
Sieve and Settling Tube Locality ______________

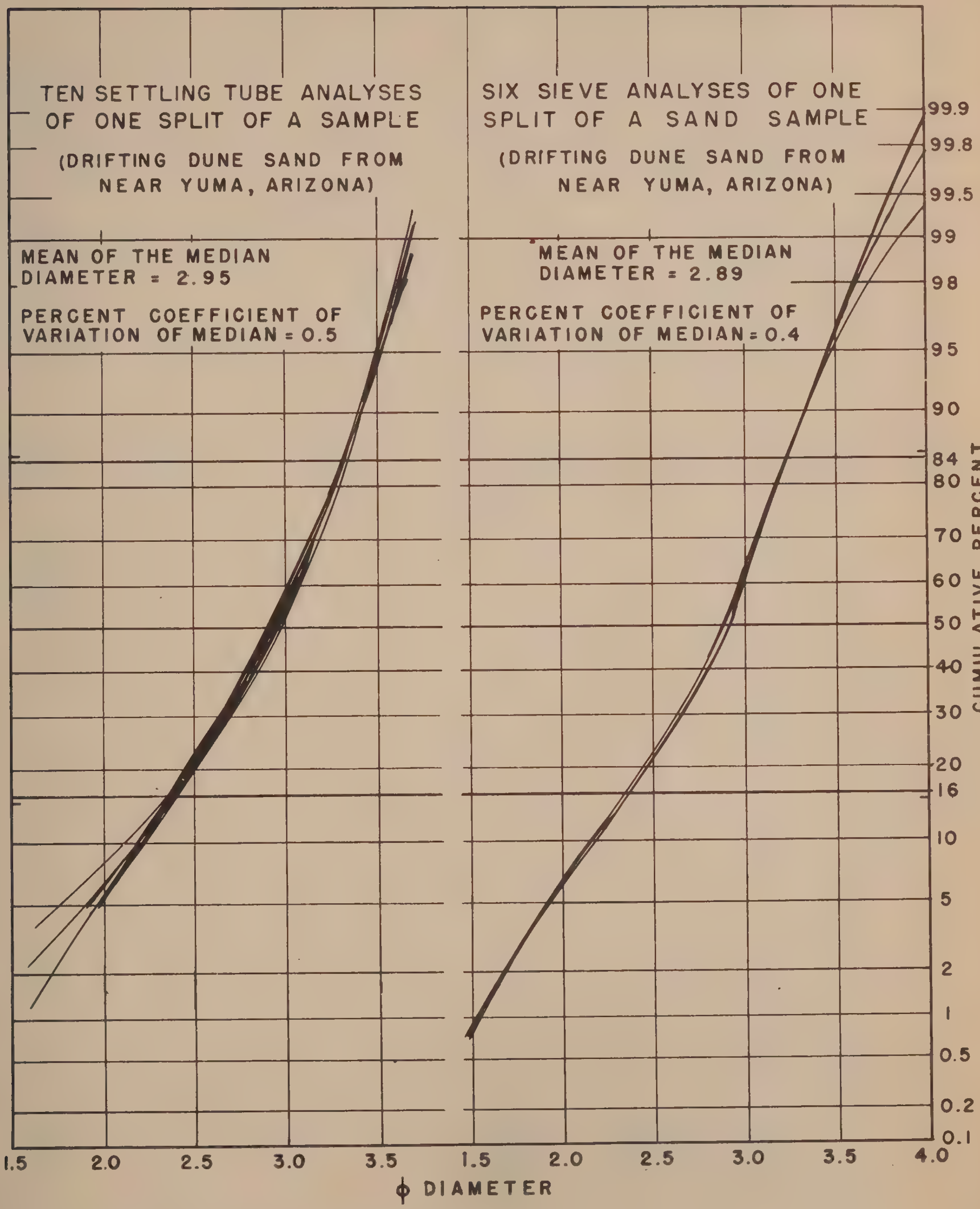
$\phi 84$ ______ | $\mathrm{Md}\phi$ =
$\phi 16$ ______
$\phi 84-\phi 16$ ___$(\frac{1}{2})$ = | $\sigma\phi$ =
$\phi 84+\phi 16$ ___$(\frac{1}{2})$ = ______
$\frac{1}{2}(\phi 84+\phi 16)-\mathrm{Md}\phi$ = S
S/ ϕ = | $\alpha\phi$ =
$\phi 95$ ______
$\phi 5$ ______
$\phi 95-\phi 5$ ___$(\frac{1}{2})$ = ______
$\frac{1}{2}(\phi 95-\phi 5)-\sigma\phi$ = K | ______
K/$\sigma\phi$ = | $\beta\phi$ =
$\phi 95+\phi 5$ ___$(\frac{1}{2})$ = ______
$\frac{1}{2}(\phi 95+\phi 5)-\mathrm{Md}\phi$ = S_2 =
S_2/ $\sigma\phi$ = | $\alpha 2\phi$ =

Dia. in ϕ	Dish No.	Wt. of Dish	Dish & Sample	Wt. of Sample	% Wt.	Tota Cum.
< -4						
$(-4)-(-3)$						
$(-3)-(-2)$						
$(-2)-(-1.5)$						
$(-1.5)-(-1)$						
$(-1)-(-0.5)$						
$(-0.5)-0$						
> 0						
Total						

Dia. in		Settling time		(Min.-sec.)		Cum. Ht. units	Cum.Ht. %	% x Wt. 1	Total Cum. %
ϕ	mm.	24°	22°	20°	18°				
0.0	1.0	13	13	13	13				
0.5	.7	15	15	15	15				
1.0	.5	18	18	19	19				
1.50	.35	24	25	26	26				
1.75	.30	29	30	31	31				
2.00	.25	37	38	39	39				
2.125	.23	41	42	43	43				
2.25	.21	46	47	48	49				
2.375	.19	53	54	56	57				
2.50	.18	57	59	1 01	1 03				
2.625	.16	1 05	1 08	1 12	1 14				
2.75	.15	1 14	1 16	1 19	1 22				
2.875	.14	1 23	1 25	1 27	1 32				
3.00	.125	1 35	1 38	1 43	1 48				
3.25	.105	2 01	2 04	2 10	2 17				
3.50	.088	2 34	2 38	2 45	2 54				
3.75	.075	3 15	3 20	3 25	3 41				
4.00	.0625	4 07	4 13	4 23	4 38				
4.25	.052	5 20	5 27	5 40	5 58				
4.50	.044	6 39	6 47	7 05	7 24				
5.00	.03125	10 42	10 51	11 10	11 48				

FIGURE 1

FIGURE 2


TEN SETTLING TUBE ANALYSES OF ONE SPLIT OF A SAMPLE
(DRIFTING DUNE SAND FROM NEAR YUMA, ARIZONA)
MEAN OF THE MEDIAN DIAMETER = 2.95
PERCENT COEFFICIENT OF VARIATION OF MEDIAN = 0.5
SIX SIEVE ANALYSES OF ONE SPLIT OF A SAND SAMPLE
(DRIFTING DUNE SAND FROM NEAR YUMA, ARIZONA)
MEAN OF THE MEDIAN DIAMETER = 2.89
PERCENT COEFFICIENT OF VARIATION OF MEDIAN = 0.4
99.9
99.8
99.5
99
98
95
90
84
80
70
60
50
40
30
20
16
10
5
2
1
0.5
0.2
0.1
CUMULATIVE PERCENT
1.5
2.0
2.5
3.0
3.5
1.5
2.0
2.5
3.0
3.5
4.0
φ DIAMETER

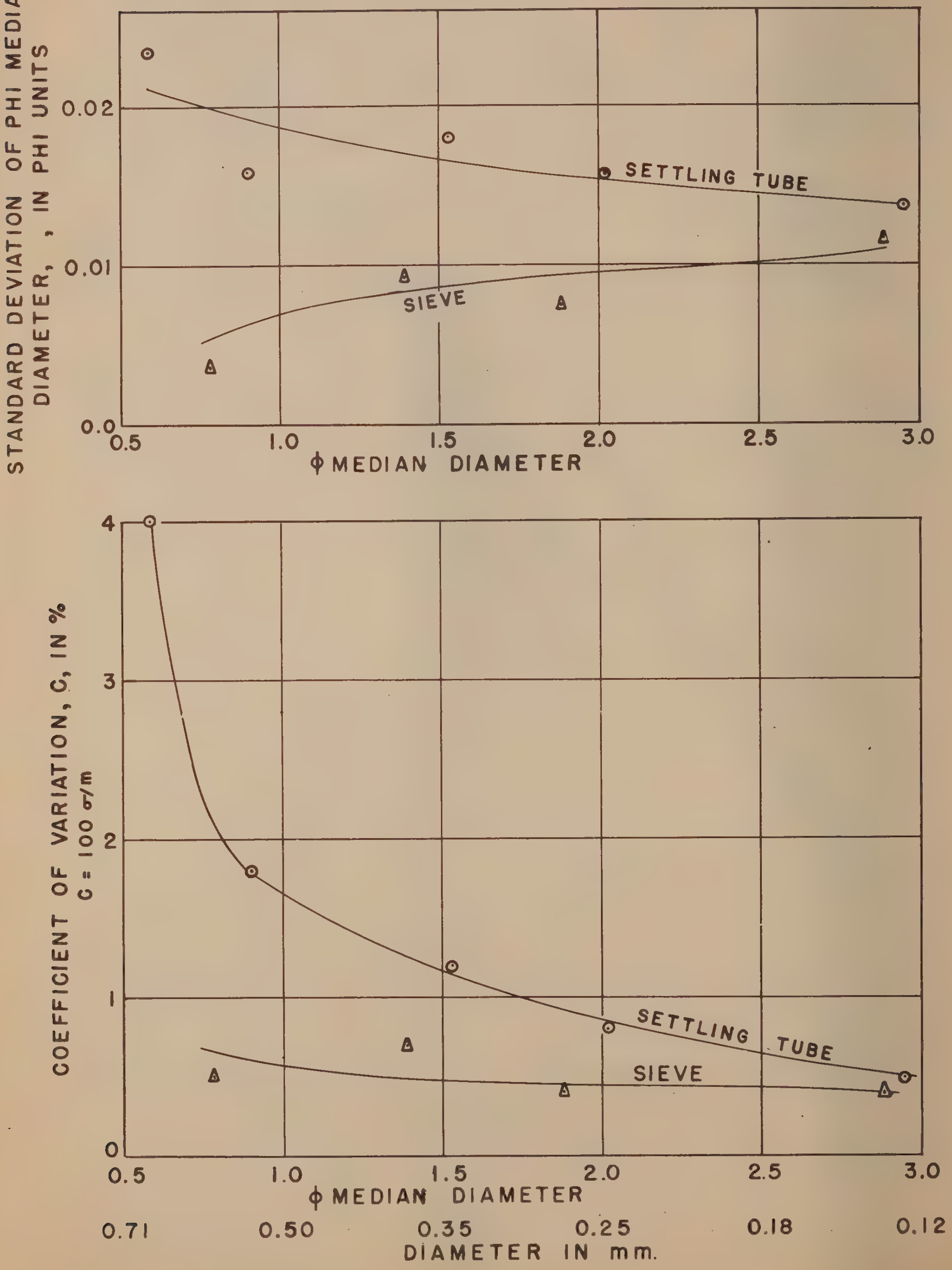
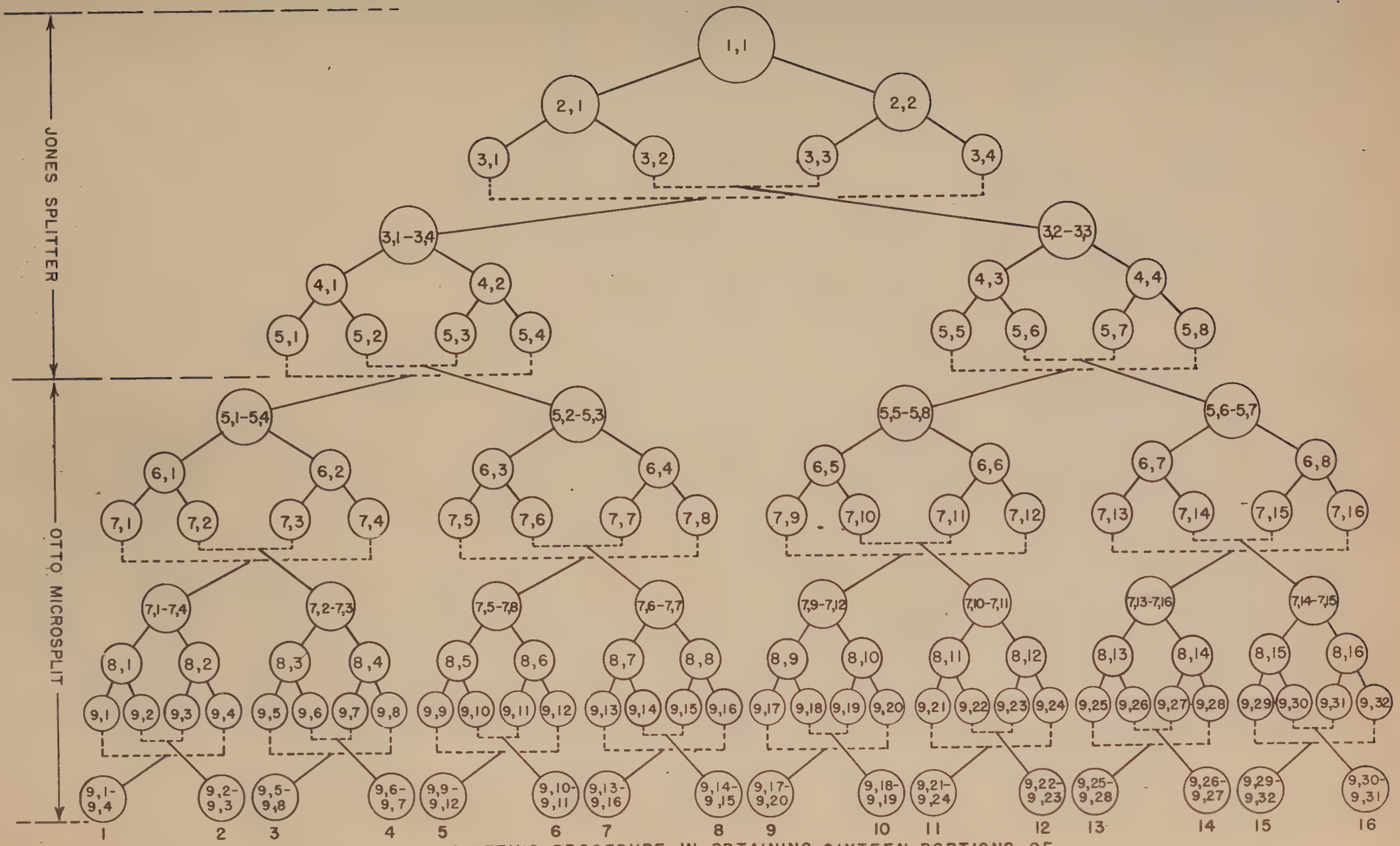


FIGURE 3

REPRODUCIBILITY OF THE SETTLING TUBE AND SIEVE ANALYSES FOR PHI MEDIAN DIAMETER

FIGURE 4


JONES SPLITTER
OTTO MICROSPLIT
1,1
2,1
2,2
3,1
3,2
3,3
3,4
3,1–3,4
3,2–3,3
4,1
4,2
4,3
4,4
5,1
5,2
5,3
5,4
5,5
5,6
5,7
5,8
5,1-5,4
5,2-5,3
5,5-5,8
5,6-5,7
6,1
6,2
6,3
6,4
6,5
6,6
6,7
6,8
7,1
7,2
7,3
7,4
7,5
7,6
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7,9
7,10
7,11
7,12
7,13
7,14
7,15
7,16
7,1-7,4
7,2-7,3
7,5-7,8
7,6-7,7
7,9-7,12
7,10-7,11
7,13-7,16
7,14-7,15
8,1
8,2
8,3
8,4
8,5
8,6
8,7
8,8
8,9
8,10
8,11
8,12
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8,14
8,15
8,16
9,1
9,2
9,3
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9,5
9,6
9,7
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9,29
9,30
9,31
9,32
9,1-9,4
9,2-9,3
9,5-9,8
9,6-9,7
9,9-9,12
9,10-9,11
9,13-9,16
9,14-9,15
9,17-9,20
9,18-9,19
9,21-9,24
9,22-9,23
9,25-9,28
9,26-9,27
9,29-9,32
9,30-9,31
1
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3
4
5
6
7
8
9
10
11
12
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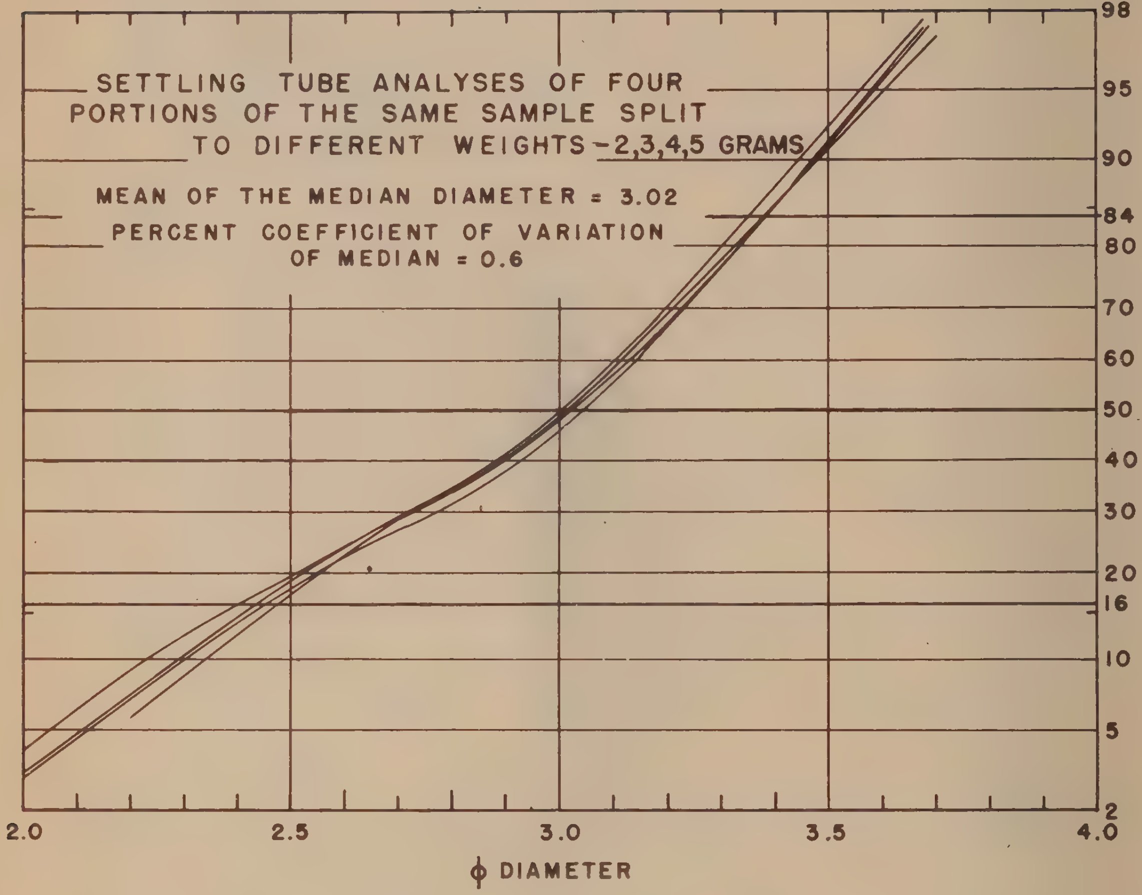
14
15
16

SPLITTING PROCEDURE IN OBTAINING SIXTEEN PORTIONS OF A SINGLE BULK SAMPLE BY COMBINING ALTERNATE QUARTERS

FIGURE 5


SETTLING TUBE ANALYSES OF FOUR PORTIONS OF THE SAME SAMPLE SPLIT TO DIFFERENT WEIGHTS–2,3,4,5 GRAMS
MEAN OF THE MEDIAN DIAMETER = 3.02
PERCENT COEFFICIENT OF VARIATION OF MEDIAN = 0.6
98
95
90
84
80
70
60
50
40
30
20
16
10
5
2
CUMULATIVE PERCENT
2.0
2.5
3.0
3.5
4.0
ϕ DIAMETER

ANALYSES OF A SAMPLE —WITH AND WITHOUT COARSE FRACTION

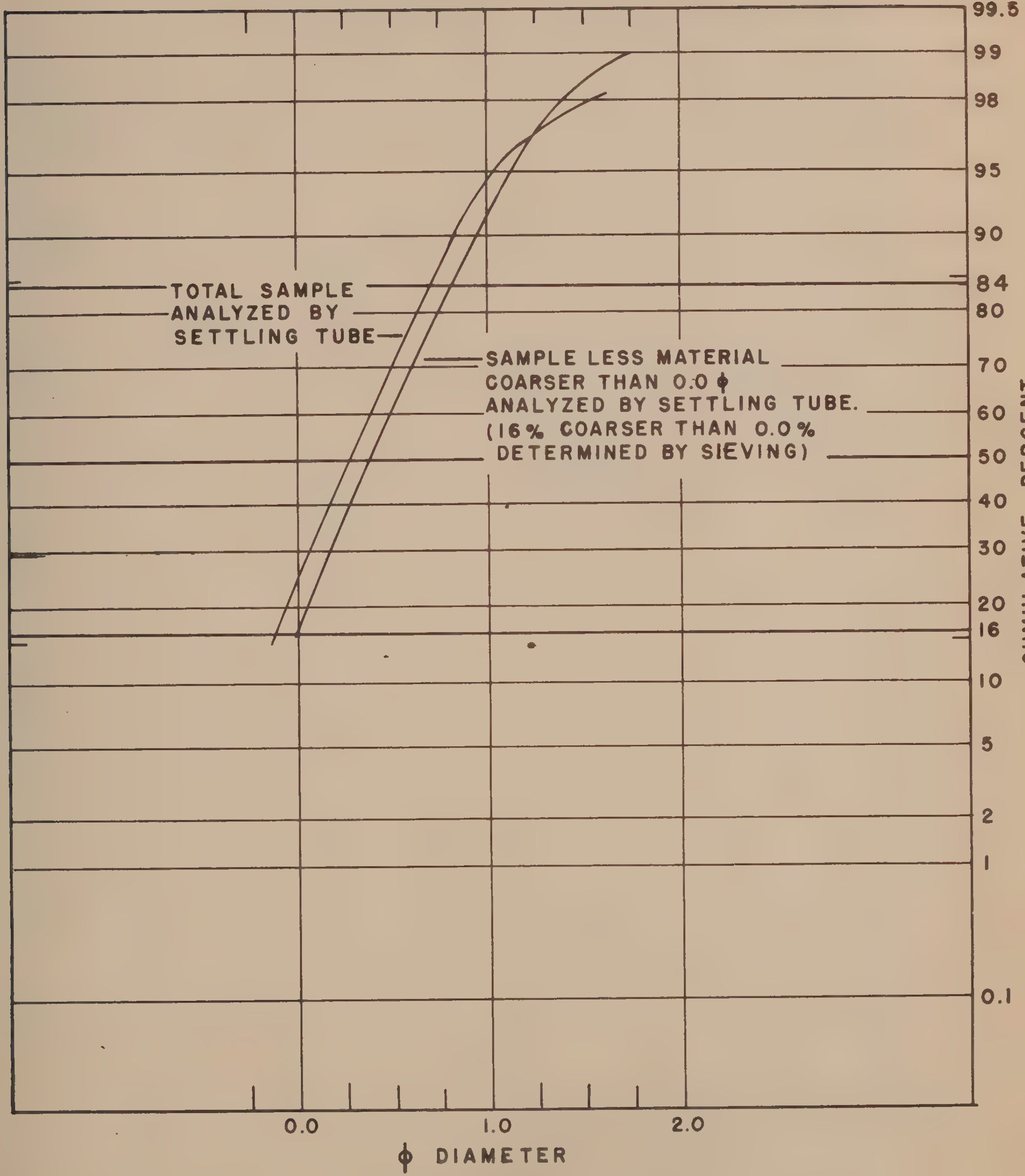
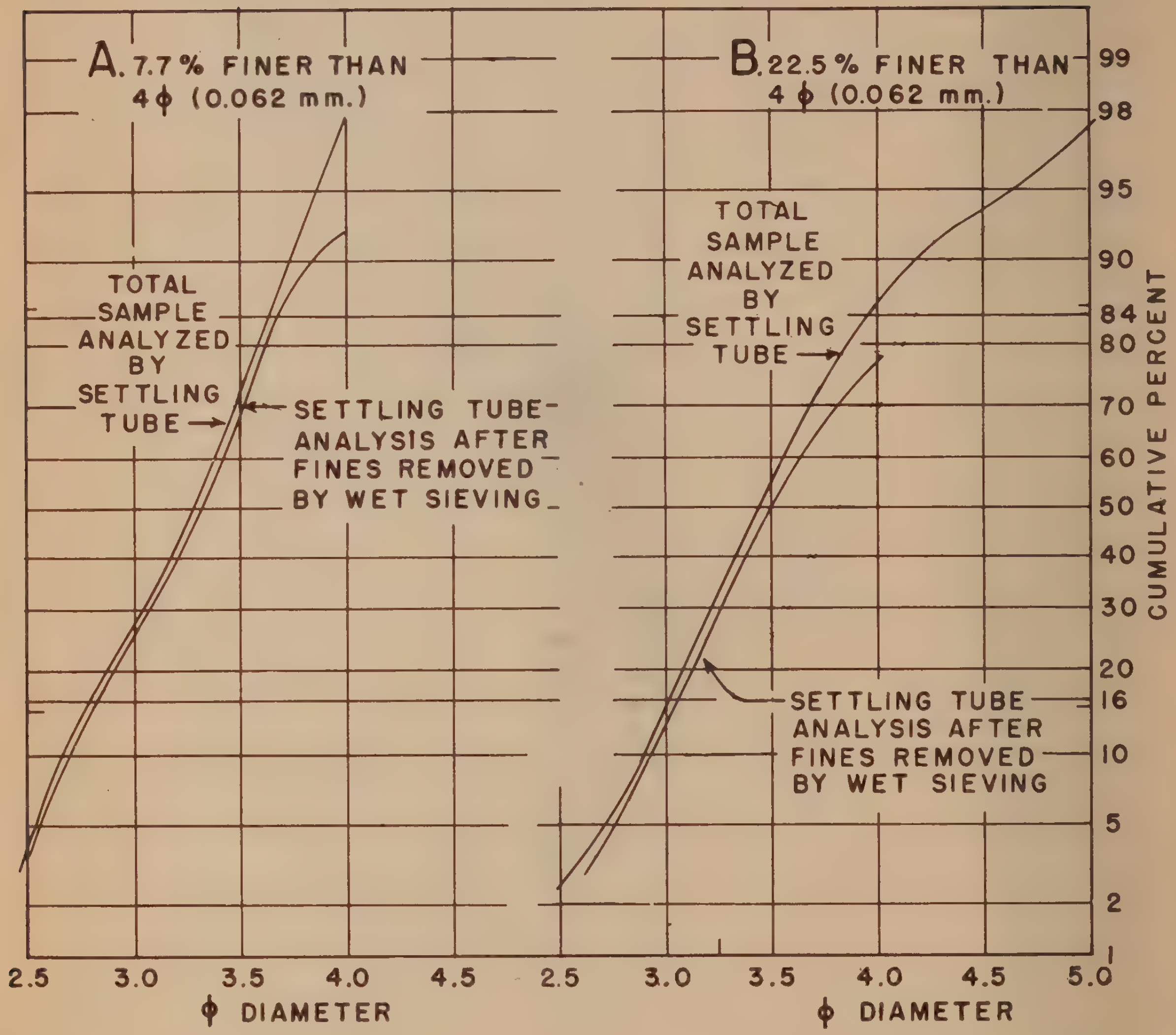


FIGURE 7

SETTLING TUBE ANALYSES OF SAMPLE— WITH AND WITHOUT FINES



514

Reprinted from SCIENCE, May 4. 1951, Vol. 113, No. 2940, pages 511–512.

itrogen Fixation by Sulfate-reducing acteria Indicated by Nitrogen/Argon atios[1]

rederick D. Sisler and Claude E. ZoBell

ripps Institution of Oceanography,
iiversity of California, La Jolla

In the course of investigations (*1*) on the utilization molecular hydrogen by autotrophic, anaerobic, sulte-reducing bacteria belonging to the genus *esulfovibrio,* evidence was obtained for the fixation free nitrogen. In preliminary experiments inverted als in pairs were placed in glass-stoppered bottles led with sea water, which served as a suitable mineral edium for the growth of H_2-utilizing sulfate reacers. One vial was filled with H_2 and the other with $_2$ as an "inert" control.

It soon became evident, however, that N_2 was not ert in the presence of hydrogenase-producing species *Desulfovibrio.* After prolonged incubation a easurable decrease in the volume of N_2 in active ltures was observed, which could not be accounted r by solubility, diffusion, or other processes involving eneral gas laws. Consequently, helium and argon ere tried as controls, both of which proved to be ert. Further investigations, based upon the decreased tios of N_2/A, confirmed the fixation of N_2 by $_2$-utilizing *Desulfovibrio.*

A pure culture of hydrogenase-producing *Desulovibrio* was used to inoculate 20 liters of inorganic a water medium overlayered with 20 liters of gas itially consisting of approximately 80% of catatically purified H_2. The remaining 20% of the gas as CO_2, N_2, and A, the latter two in a ratio of 1 art of A to 83 parts of N_2. The composition of the gas was determined periodically by means of mass spectrometer analyses.[2]

The growth or reproduction of the bacteria was accompanied by a decrease in the H_2 and CO_2 content of the gas phase, as appreciable quantities of these two components were consumed by the autotroph

$$2H_2 + CO_2 \rightarrow (HCHO) + H_2O,$$

where (HCHO) represents a primary building block of bacterial cell substance, not necessarily formaldehyde. The content of CO_2 in the gas phase was also affected by the pH of the medium, which became more alkaline as sulfate was reduced to sulfide:

$$4H_2 + H_2SO_4 \rightarrow H_2S + 4H_2O.$$

As a result of H_2 and CO_2 uptake, the concentration of N_2 and A in the gas phase increased (Table 1), but the decreasing N_2/A ratio indicated that N_2 was being consumed by the autotrophic bacteria. This was confirmed by determining the absolute quantities of each gas in the closed system. The small amount of

TABLE 1

CHANGE IN COMPOSITION OF GAS CAUSED BY AUTOTROPHIC SULFATE REDUCERS GROWING IN 20 LITERS OF INORGANIC MEDIUM OVERLAYERED WITH 20 LITERS OF GAS AT 28° C

Component	Composition of gas after		
	2 days (%)	42 days (%)	61 days (%)
H_2	82.93	56.04	47.42
O_2	0	0	0
CO_2	0.51	0.27	0.19
H_2S	0	0	0.1
N_2	16.63	43.14	51.61
A	0.20	0.55	0.68
N_2/A ratio	83	78	76

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[1] Contribution from the Scripps Institution of Oceanogaphy, New Series No. 514. This investigation was suported in part by a grant from the American Petroleum nstitute, Research Project 43A.

[2] The mass spectrometer analyses were made by the Richfield Oil Corporation, Wilmington, Calif. The writers also acknowledge the valuable suggestions of D. L. Fox, E. D. Goldberg, and N. W. Rakestraw.

H_2S appearing in the gas phase is attributable to its absorption by the slightly alkaline medium.

Four other pure cultures of H_2-utilizing sulfate-reducing bacteria incubated at 28° C in mineral salts solution overlayered with a mixture of H_2, CO_2, N_2, and A yielded the results that are shown in Table 2.

TABLE 2

Culture No.	N_2/A ratio after	
	2 days	60 days
45: 268-1	83	67
45: 268-2	83	76
45: 268-3	83	79
45: 268-4	83	55
None (control)	83	83

These observations, coupled with the observed growth of the bacteria in mineral salts solution containing N_2 as the sole source of nitrogen, establish the ability of another physiological group of bacteria to
fix N_2. Being widely distributed in marine sediment
(*1, 2*), such bacteria may play an important part i
the fixation of N_2 in the sea.

The observations help to substantiate the predictio
of Lindstrom *et al.* (*3, 4*) that all hydrogenase-pro
ducing bacteria fix N_2. These workers employed micro
Kjeldahl and tagged-atom (N_2^{15}) techniques t
demonstrate the fixation of N_2 by *Chromatium*
Chlorobacterium, and *Rhodospirillum* species. W
recommend following the N_2/A ratios of gas mixture
which can be easily and accurately determined b
mass spectrometer, as an indicator of the ability o
bacteria to fix N_2.

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2. ZOBELL, C. E. *Bull. Am. Assoc. Petroleum Geol.*, **31**, 170 (1947).
3. LINDSTROM, E. S., BURRIS, R. H., and WILSON, P. W. *Bact.*, **58**, 313 (1949).
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Särtryck ur Tellus, vol. 3, nr 1, 1951

SHORTER CONTRIBUTION

Note on the Dynamics of the Antarctic Circumpolar Current[1]

By W. H. MUNK[2] and E. PALMÉN[3]

Abstract

Unlike all other major ocean currents, the Antarctic Circumpolar Current probably does not have sufficient frictional stress applied at its lateral boundaries to balance the wind stress. The balancing stress is probably applied at the bottom, largely where the major submarine ridges lie in the path of the current. The meridional circulation provides a mechanism for extending the current to a large enough depth to make this possible.

Under the assumption that the wind stress on the sea surface is balanced by the frictional stress against the sides of the ocean basins one can arrive at a fairly satisfactory picture of the large scale circulation in various oceans (MUNK, 1950; MUNK and CARRIER, 1950). The computed transports differ at most by a factor of two from the observed transports. In the case of the Antarctic Circumpolar (AC) current a similar reasoning leads however to a computed transport one hundred times the observed transport.

In its simplest form we may regard the AC current as an eastward flow on a plane tangent to the earth at the South Pole. The flow is induced by constant eastward winds, and depends only on the distance r from the pole on this plane. In this system a balance between the wind stress τ and the lateral friction is expressed by

$$\tau + A \frac{d}{dr}\left(\frac{dM}{dr} + \frac{M}{r}\right) = 0$$

where A is the lateral kinematic eddy viscosity and M the eastward mass transport across a normal vertical plane of unit width extending from surface to bottom.[4] The solution which vanishes at the Antarctic continent ($r = r_0$) and at some other latitude ($r = r_1$) is

$$M = \frac{\tau}{3A} r (r - r_0)\left(\frac{r + r_0}{r_1 + r_0}\,\frac{r_1^2}{r^2} - 1\right).$$

The total AC transport equals

$$T = \int_{r_0}^{r_1} M\,dr =$$

$$= \frac{\tau}{18A}\left(r_1^3 - r_0^3 - \frac{6\,r_1^2\,r_0^2}{r_1 + r_0}\ln\frac{r_1}{r_0}\right).$$

Setting $\tau = 2$ dynes cm^{-2}, $A = 10^8$ cm^2 sec^{-1}, and placing the boundaries at 70° S and 45° S latitudes gives $T = 5 \times 10^{16}$ g sec^{-1}. At the narrowest section, Drake Passage, the boundaries are at 65° S and 55° S latitudes, and $T = 10^{15}$ g sec^{-1}. The observed transport is 10^{14} g sec^{-1}. The discrepancy is not materially altered by more elaborate calculations involving spherical coordinates and allowing for a variation of wind with latitude.

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[1] Contribution from the Scripps Institution of Oceanography, New Series No. 515. This work has been supported by a contract with the Office of Naval Research.

[2] Institute of Geophysics and Scripps Institution of Oceanography, University of California.

[3] Academy of Finland.

[4] Strictly speaking we should replace the relative transport M by the absolute transport $M + \omega r h$, where ω is the earth's angular velocity and h the ocean depth. However, the second term which represents solid rotation drops out upon differentiation.

Among the possible explanations for the discrepancy are:

1. The value of A pertaining to the AC may have been taken too small, and should possibly be one to two orders of magnitude larger than 10^8 cm^{2}sec^{-1}. Various methods for other large scale ocean currents have led to values from 10^7 to 10^8 cm^2 sec^{-1}.

2. The wind stress is balanced by stress against the bottom, rather than against the lateral boundaries as has been assumed. Somewhat artificially we may divide this bottom effect into (2a) skin friction, and (2b) the mountain effect.

2a. A bottom velocity so great that the wind stress is balanced entirely by skin friction, is given by Sverdrup et al. (1942, p. 480),

$$v_b = 2{,}5\sqrt{\frac{\tau}{\varrho}}\,\ln\left(\frac{z+z_0}{z_0}\right).$$

Setting $\tau = 2$ dynes cm^{-2}, $\varrho = 1.0$ g cm^{-3}, $z_0 = 2$ cm, and $z = 100$ cm gives $v_b = 14$ cm sec^{-1} at 100 cm above bottom. This is approximately the maximum surface velocity. The value for the "roughness length" z_0 is based on unpublished measurements by Revelle and Fleming in San Diego Harbor. But this process could at best lead to a linear velocity gradient between top and bottom of 14 cm sec^{-1}/4 km $= 3.5 \cdot 10^{-5}$ sec^{-1}. In order for the resulting vertical stress, $3.5 \cdot 10^{-5} A_v$, to equal a wind stress of 2 dynes cm^{-2} at the surface the vertical eddy viscosity A_v would have to equal $6 \cdot 10^4$ g cm^{-1} sec^{-1}. Reported values are generally less than $2 \cdot 10^3$ g cm^{-1} sec^{-1} in the upper few hundred meters, and even less at greater depth (Sverdrup et al. 1942, p. 482).

2b. The foregoing equation refers to the statistical effect associated with "small" irregularities in the sea bottom. In meteorology, the mountain effect associated with the few largest irregularities on the earth's surface has been found at least as effective as skin friction (Widger, 1949), but in oceanography the mountain effect has been neglected. Let dh/dx denote the eastward (down current) slope of the sea bottom. The eastward component of force exerted on an element of bottom of area ds equals

$$p_b\ (dh/dx)\ ds,$$

where p_b is the pressure along the bottom. For small slopes, ds can be taken as the area projected on a horizontal plane. The net effect around a circle of latitude of circumference C vanishes if the pressure is constant ($\int_c dh = 0$), or if the depth is constant ($dh/dx = 0$). If however the bottom pressure on the up current side exceeds on the average the pressure at the same level on the lee side by Δp_b, then the stress has a mean value of the order of

$$\frac{1}{C}\,\Delta p_b\ \Delta h$$

which could balance the mean wind stress. Here Δh is the sum of the heights of the sea mounts. At 60° S the current encounters the Kerguelen ridge (3 km), the Macquarie ridge (2 km), the South Pacific ridge (1 km), and the South Antillean arc (4 km). The currents must diminish over each ridge and accelerate between ridges, but on the average the mountain effect may balance the wind stress. Setting $\Delta h = 10$ km, $\mathcal{C} = 18{,}000$ km, $\tau = 2$ dynes cm^{-2} gives $\Delta\, p_b \approx 4{,}000$ dynes cm^{-2} $= 4$ dynamic centimeters. At the surface the horizontal variations in pressure are of the order of a dynamic meter, with the larger values occurring on the up current side. The wind stress can therefore be accounted for by horizontal pressure gradients at the bottom similar in phase to those observed near the surface, and amounting to a few percent of the surface gradients.

If the wind stress is to be balanced by stresses along the sea bottom, the AC current must be deep enough to reach to the bottom. Sverdrup has pointed out that the sharp leftward displacement of the surface current over the submarine ridges would indicate that this is the case (Sverdrup et al, 1942, pp. 466—469). We may consider two possible explanations:

1. Each layer induces, by turbulent interchange of momentum, motion in the layer beneath, and in this manner the wind stress is transmitted to the sea bottom. Because the fetch of the wind is essentially infinite this mechanism is more effective in the AC current than elsewhere.

2. The meridional circulation exports absolute angular momentum in the upper layer, and imports it in a lower layer. Suppose the loss of angular momentum in the upper layer alone associated with a flow of Q g sec^{-1} northward across the 45° S parallel of latitude is balanced entirely by the wind *torque* over the ocean between the Antarctic continent (70° S) and 45° S:

$$Q\ (\omega\ R \cos 45^\circ)\ (R \cos 45^\circ) =$$

$$= \int_{45^\circ\,\mathrm{S}}^{70^\circ\,\mathrm{S}} \tau\ (2\,\pi\, R^2 \cos\varphi)\ (R\cos\varphi)\ d\,\varphi,$$

where ω is the earth's angular velocity and R its radius. Setting $\tau = 2$ dynes cm^{-2} leads to $Q = 3 \times 10^{13}$ g sec^{-1}. This value is in agreement with the observed northward transport in the upper 500—1,000 meters, due mostly to the Benguela and Peru Currents. If we suppose for the moment that the difference between precipitation and evaporation over the whole region south of the latitude 45° S and in addition a possible decrease of the Antarctic ice cap could provide all this water, then the wind stress could be accounted for by the export of absolute angular momentum into the southern oceans. Actually not more than about 0.3—0.5 per cent of the above value of Q could be provided in this way[5], so that virtually all of the water lost in the upper layers must be returned to the Antarctic Sea at a lower level[6], apparently at depths between 1,000 and 4,000 meters. Conservation of angular momentum then requires an increasing cyclonic (eastward) circulation at these great depths with decreasing distance from the pole. Deacon's analysis of the *DISCOVERY* observations in fact shows a remarkably uniform horizontal density gradient throughout most of the water column, whereas, for example, Iselin's sections across the Gulf Stream reveal a sharp decrease in horizontal gradients at a thousand meters (compare figs. 159 and 186, SVERDRUP et al. 1942). From this point of view the principal action of the wind is not so much to induce cyclonic circulation throughout the water column, as to prevent anticyclonic circulation of the northward drifting surface waters.

To summarize: deep water in the Antarctic ocean drifting towards the axis of the rotating earth develops an easterly (relative) flow. The retarding pressure of the submarine ridges against the deep current balances the stress exerted by the wind on the water's surface.

The foregoing speculation regarding the dynamics of the AC current would make it differ radically from other major ocean current systems, which are limited essentially to the upper 1,000 meters, and for which the stresses against the lateral boundaries are adequate to balance the wind stress. The difference is due largely to boundaries which prevent the zonal flow of water around the earth. Assume that the Drake Passage should close, and that the Macquarie Ridge should emerge from the surface. Then the water in the confined sector would pile up against the downwind boundary. If the wind blows with equal strength at all latitudes, the resulting horizontal pressure gradient will balance the wind stress and there would be no circulation involving a horizontal gyre. If however the winds at higher latitudes are weaker or, as is the case, reverse in direction, the resulting wind torque would set up a gyre within this confined sector of the Antarctic Ocean. As an example, the Gulf Stream is the western component of a "subtropical gyre" maintained by the easterly winds to the south and the westerly winds to the north. In a confined ocean the transport depends therefore on the curl of the wind stress (MUNK, 1950); in a zonal (Antarctic) ocean the transport has been shown here to be proportional to the wind stress itself.

We have also shown the transport in a zonal ocean to vary as A^{-1} provided the wind stress is balanced by lateral friction. In a confined ocean where such a balance does in fact exist the transport is independent of A (MUNK, 1950)! This surprising result has to do with the west-east asymmetry induced by the earth's rotation on a confined gyre. The center of the gyre (Sargasso Sea) is displaced to the west, and the western current (Gulf Stream) is pressed against the boundary. If A is very large, this asymmetry, and hence the shear against the western boundary, are small. If A is relatively small the asymmetry is very pronounced, and the shear very large. The product of A times the shear, i. e., the lateral friction, remains the same, and is so large in this western region that it almost balances the wind stress over the entire subtropical gyre.

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[5] Provided a reported secular rise in world-wide sea level by 1 mm per year is due alone to melting in the Antarctic.

[6] An additional complication is the northward flow along the bottom of the heavy water formed near the Antarctic continent during freezing, and accounting for most of the bottom water in deep basins the world over.

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Reprinted from ENDOCRINOLOGY
Vol. 48, No. 4, April, 1951
pp. 485-488

ACCUMULATION OF RADIOIODINE IN THE THYROID GLAND OF ELASMOBRANCHS[1]

The incorporation of iodine into the thyroxin of the thyroid glands of man and other higher vertebrates has been well demonstrated, but little is known of these relations in the lower vertebrates. Gorbman and Creaser (1942) demonstrated that the endostyle of larval lampreys (ammocetes) can accumulate this element, but they did not mention the concentration of iodine in the adult. Recent development of emulsion-tissue radioautography (Bélanger, 1950) enables us conveniently to demonstrate that the elasmobranch fishes can also concentrate iodine in their thyroids. Elasmobranchs, in contrast with teleosts, possess a large and easily recognized discrete thyroid gland (Gudernatsch, 1911; Ferguson, 1911), which consists of a mass of vesicular follicles lying behind the posterior border of the mandible and resting on the coracohyoid muscle.

In this study three species were used, a shark, *Mustelus californicus*, and two rays, *Zapteryx exasperata* and *Holorhinus californicus*. All were seined near La Jolla, California, and were kept in a cement aquarium with running sea water several days before receiving 400 microcuries of I^{131} intramuscularly near the dorsal fin.[2] Forty-six hours after injection, the thyroid glands were dissected out, and the radioautographic slides were made by the inverted autograph procedure (Bélanger, 1950), in which the emulsion is combined with the tissue on the slide.

Received for publication February 12, 1951.

[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 516. Received for publication February 15, 1951.

[2] The I^{131} used in this investigation was supplied by the Oak Ridge National Laboratory on allocation from the Isotopes Division, U. S. Atomic Energy Commission.

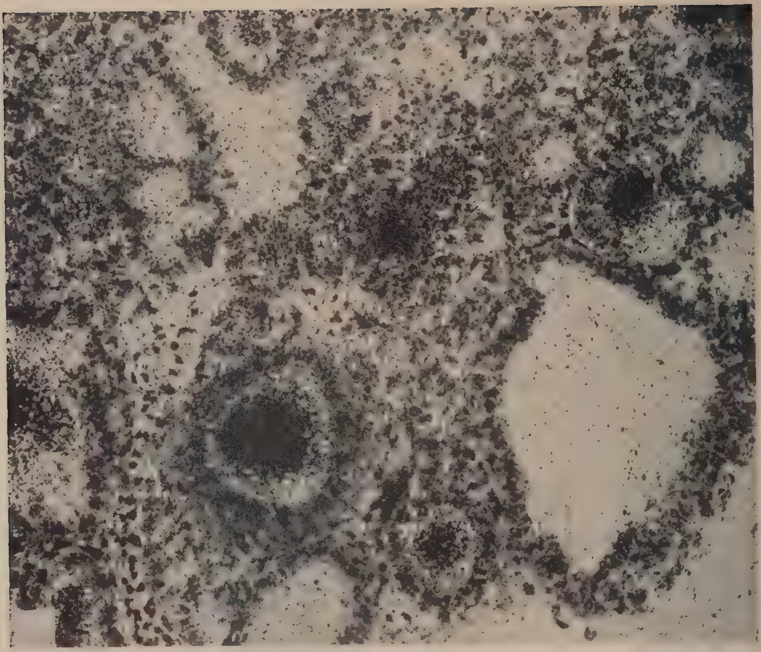

Fig. 1. Portion of thyroid gland of mottled guitarfish (*Zapteryx exasperata*), sacrificed 46 hours after an intramuscular injection of radioiodine. The radio-element is concentrated at the lumen of the follicles. Hematoxylin-eosin. ×300.

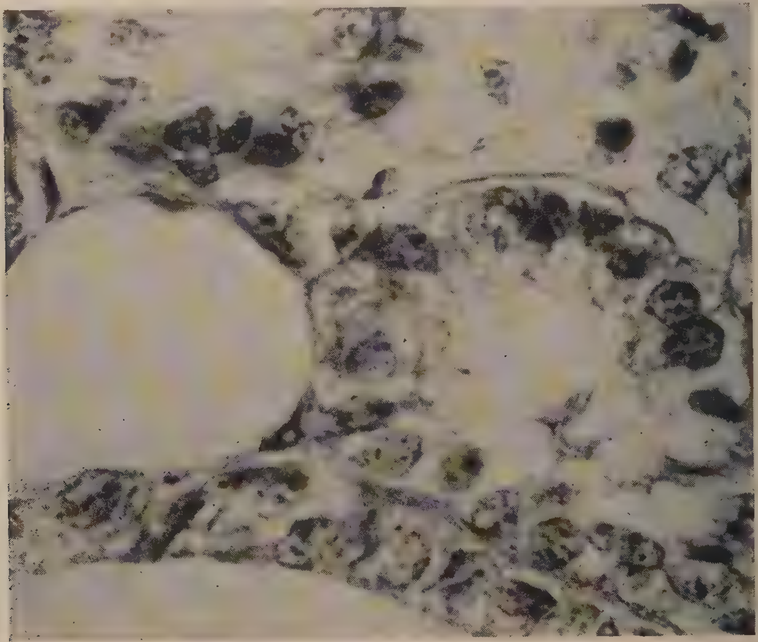

Fig. 2. One small follicle closely adjacent to portion of a large follicle in a thyroid gland of gray smoothhound (*Mustelus californicus*). Note most of the follicular nuclei are faint in Feulgen stain. ×920.

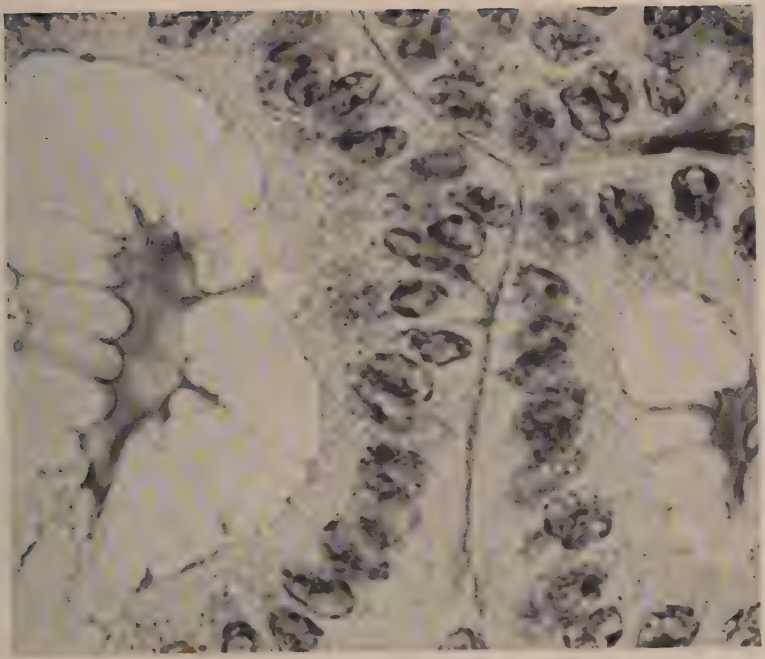

FIG. 3. Three adjacent follicles of an iodine-concentrated thyroid of *Zapteryx exasperata*. Note that the chromatin materials of the follicular nuclei condensed and adhered to the nuclear membranes, and that the nuclear membranes are folded. Feulgen stain. ×910.

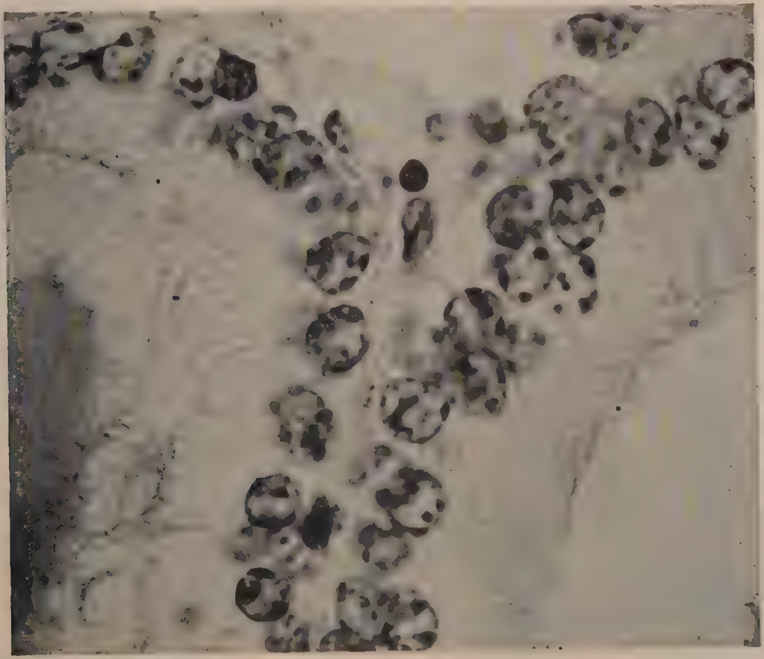

FIG. 4. Portion of two adjacent follicles of a postmortem thyroid taken from a *Zapteryx exasperata* shortly after death. Note that the heterochromatin is highly condensed and intensely stained by the Feulgen dye. ×920.

The vesicles of the elasmobranch thyroids are lined by epithelium of a low columnar type, containing colloid. In the emulsion-tissue slide, little assimilation of iodine is shown in the follicular epithelium. More conspicuous, often, but markedly variable is the concentration of radioiodine in the follicles. In adjacent follicles the uptake of the radioiodine varies greatly (Fig. 1). In general the smaller follicles contain much radioiodine and sharply contrast with adjacent large follicles, which accumulate little iodine. In the same gland the larger follicles may contain more colloid with slight activity, while the smaller ones contain less colloid but more iodine. This may indicate, in the elasmobranchs as in other vertebrates, that the volume of colloid in the thyroid follicles cannot be regarded as a reliable index of the activity of the secretory epithelium. An estimate of the secretory activity of the glandular follicles could be based on the concentration of radio-activity shown in the inverted autograph (Fig. 1).

Destruction of normal thyroid gland by the administration of I^{131} has been reported in higher vertebrates (Goldberg, Chaikoff, Lindsay, and Feller, 1950, with references). The 400-microcurie dose of this isotope in the elasmobranch thyroid similarly induced swelling and vacuolation of the cytoplasm of many epithelial cells. Degenerative changes were also visible in the nuclei. The nuclear membrane became folded and wrinkled, as it did in the rat thyroid as described by Goldberg, *et al.* In the normal thyroid gland, as determined in *Mustelus californicus*, the chromatin materials of the nucleus were less basophilic and were faint to the Feulgen test (Fig. 2), obviously because of the prevalence of ribonucleic acid in the nucleus. However, in the follicular nucleus of the irradiated thyroid of *Zapteryx*, some chromatin was condensed into a little lump of the Feulgen-positive desoxyribonucleic acid adhering to the nuclear membrane (Fig. 3). This phenomenon became more manifest as the heterochromatin lumps were highly condensed and intensely stained by the Feulgen dye, as was seen in a thyroid taken from a *Zapteryx* shortly after death (Fig. 4).

Radiation is known to produce minute nuclear and cytoplasmic changes. The first effect seems to be the transformation of ribonucleic acid into desoxyribonucleic acid, and involves a reversible inhibition of the synthesizing abilities of desoxyribose acid within the cells. With this inhibition the supply of ribose nucleotides to the cell metabolism would depend on the synthesis of cytoplasmic proteins. But the radiation probably would exert the same degenerating effect in cytoplasm. The cytoplasmic ribonucleic acid supply to the nucleoprotein synthesis can no longer be metabolically interchangeable, thereby initiating the cellular degeneration process in the thyroids.

The authors wish to acknowledge the advice of Dr. Carl L. Hubbs and the aid given by Mr. Carl Oppenheimer in the photomicrographs.

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THE ESTIMATION OF DISSOLVED PHOSPHATE IN SEA WATER[1,2]

By

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ABSTRACT

The molybdenum-blue method of determining dissolved inorganic phosphorus in sea water was modified for use with a photoelectric colorimeter. The effect of reagent concentration, time, and temperature on the rate and extent of color development was studied. Practical suggestions are given for carrying out routine analyses at sea.

INTRODUCTION

The molybdenum-blue method for determination of dissolved inorganic phosphorus in sea water has been in use for many years. Modifications have been made in the conditions of analysis (size of sample, reagent concentration, time of standing, and temperature) and in the methods of making the colorimetric comparison of standard and unknown samples.

In recent years attempts have been made to adapt the method for use with photoelectric colorimeters. Harvey (1948) has made a careful study of the method with a photoelectric colorimeter of his own design.

In 1948 it became evident that work of the Marine Life Research program of the Scripps Institution of Oceanography would require that large numbers of routine phosphate determinations be carried out at sea by semiskilled personnel. A preliminary study showed that further modification of the method and a better understanding of the effect of various factors on the reaction would be required in order that data obtained by various people on different ships be consistent and reliable. This paper presents the results of this work on the phosphate method, carried out during the last two years.

Absorptimetric terms and symbols used are those adopted by the National Bureau of Standards and described in Letter Circular LC-857 of the National Bureau of Standards (1947).

APPARATUS

All spectrophotometric measurements were made in a Beckman Model DU Quartz Spectrophotometer with 10-cm absorption cells having COREX windows. Certain photometric estimations of phos-

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[1] This work has been supported by the Marine Research Committee of the State of California.

[2] Contribution New Series No. 517 from the Scripps Institution of Oceanography.

Reprint from SEARS FOUND. JOURN. MAR. RES.

phate were also made in a photoelectric colorimeter, the Automatic Servo-operated Photometer (ASOP) to be described elsewhere. In this instrument monochromatic light was obtained with interference-type filters peaked at a wavelength of 700 mμ;[3] 10-cm absorption cells were used, the instrument usually being balanced against an air light-path rather than against an absorption cell filled with the solvent. A correction was applied for absorbancy of the cell and solvent.

Reagents were added either from micro-burets or from specially designed reagent dispensers to be described elsewhere.

FORMATION OF MOLYBDENUM-BLUE

Addition of a small quantity of a sulfuric acid solution of ammonium molybdate to a sample of water containing phosphate ions results in formation of a phosphomolybdate complex. Subsequent reduction with an acid solution of stannous chloride produces a blue color, the intensity of which varies with the concentration of phosphate ions initially present. The rate at which color forms and then fades and the intensity of the color formed depend also on the concentration of reagents and on the temperature and salinity of the sample.

Robinson and Wirth (1935), using either Atkins or Truog-Meyer reagents, found that the maximum intensity of color occurred seven minutes after addition of reagents, but they observed no fading until after an hour. More recently, Robinson and Thompson (1948) found that the maximum color intensity developed in about seven minutes, but they made no statement about duration of this maximum intensity.

In this laboratory, the formation of molybdenum-blue was studied by adding reagents to a sample and by transferring the sample to an absorption cell which was immediately placed in the spectrophotometer. Readings of transmittancy were made at frequent intervals; during intervals when readings were not being made, the absorption cell was out of the light path and hence in the dark. In a study of the reagents used by Wattenberg (1937), essentially the same as those employed by Robinson and Thompson (1948), it was found that in sea water color developed within 5 minutes to within 2% of maximum absorbancy, remained within 2% for about 10 minutes, then faded.

It was desirable to extend the flat part of the curve so that large numbers of samples could be analyzed efficiently at sea. Harvey (1948) showed that adding increased quantities of stannous chloride increased the rapidity of color development, delayed the onset of

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[3] Although Harvey (1948) states that the blue substance produced in distilled water has a different light absorption band from that produced in sea water, the absorption spectrum studied with the spectrophotometer showed peak absorbancy at 700 mμ in distilled water, in 3.3% NaCl solution, and in sea water.

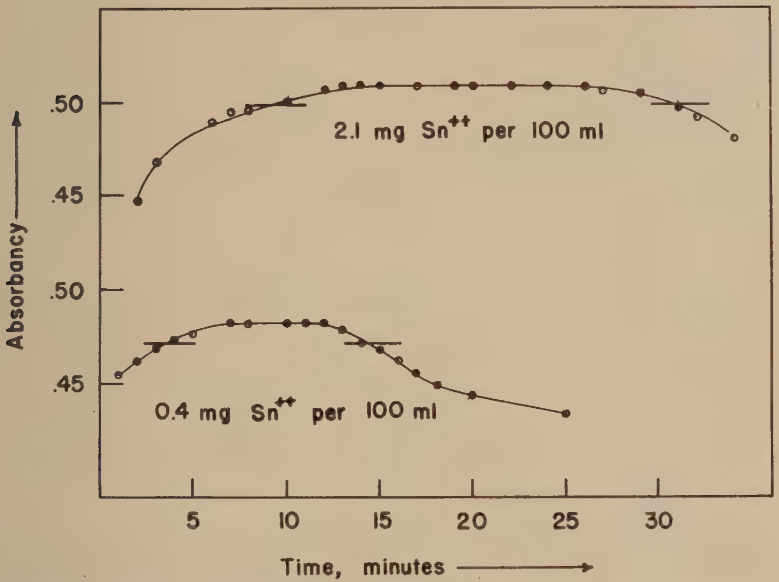

Figure 1. Effect of concentration of stannous tin on stability of molybdenum-blue. Samples are sea water with 1.5 µg at/L of added PO_4-P.

fading, and increased the amount of color formed with a given quantity of phosphate. He used concentrations of 0.43 to 0.64 mg Sn^{++} per 100 ml of sample; most workers have used concentrations approximating these.

The maximum practicable tin concentration seems to be about 2.1 mg Sn^{++} per 100 ml sample; upon further increase, reagent blanks develop a colloidal precipitate of tin oxides and are unreadable. With this concentration of tin, color develops within 10 minutes to within 2% of maximum absorbancy and remains within 2% for 20 minutes (Fig. 1). With such a long period of time during which the absorbancy remains constant, it is possible to make large numbers of determinations rapidly, scheduling additions of reagents and readings of absorbancy without waste of time.

Objection has been raised to increased tin concentration on the grounds that a yellow coloration appears and interferes with readings. This color is evident particularly with low phosphate concentrations and with the long absorption paths customarily employed in visual colorimetry. When measurements are made at the peak absorbancy

(700 mμ) in a photoelectric colorimeter there is no evidence of interference. Linearity of standardization curves with this tin concentration is evidence that the discoloration, if present, does not interfere with accuracy.

In addition to an increase in the period of time during which readings can be made, an increase in the tin concentration increases the sensitivity of the method. However, this increase is not as great as that resulting from an increase in the absorption cell length from 10 cm to 15 cm.

TABLE I.—EFFECT OF MEDIUM ON DURATION OF MAXIMUM ABSORBANCY

Concentration added PO_4-P	*Duration of maximum absorbancy**		
	Dist. water	*3.3% NaCl*	*Sea water*
μg at L	Min.	Min.	Min.
0.6	6–19.5	7–32	9–31
3.0	1– 8.5	6–17	8–26

* Time after addition of reagents during which absorbancy is within 2% of its maximum value. Sea water salinity approximately 33 °/oo.

The rate of color formation and the amount of color formed are also affected by the phosphate content and by the salinity of the sample. Maximum absorbancy is attained more slowly and persists longer in samples with low phosphate content. However, if color is considered constant while it is within 2% of maximum absorbancy, it is found that, in sea water, color is constant at all but the highest concentrations of phosphate (greater than 2.4 μg at/L) from 10 minutes until 30 minutes after reagents are added. At higher phosphate concentrations, color is constant only until 25 minutes after reagents are added.

When reagents are added to either distilled water or to a 3.3% sodium chloride solution containing added phosphate, the rate of color formation is much more sensitive to phosphate content than is that of a sea water dilution (see Table I). The molybdenum-blue color is more stable in sea water than in either salt solution or distilled water.

The rate of color development and the amount of color formed are also affected by the temperature of the sample. At a lower temperature, maximum absorbancy is not attained so rapidly and is not so great as that at a higher temperature. Thus, as temperature increases, the slope of the standardization curve, hence the sensitivity of the method, increases.

If a series of standardization curves is run at different temperatures and if the absorbancy index of each curve is plotted as a function of temperature, it is found that the absorbancy index varies linearly with

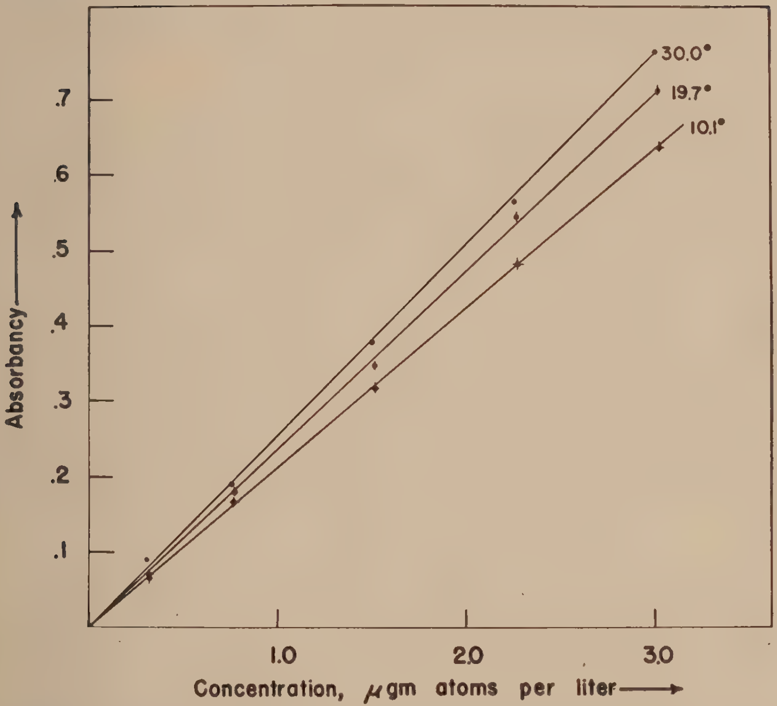

Figure 2. Phosphate standard curves at various temperatures, using sea water with added phosphate. These curves have been passed through the origin to emphasize the change in slope.

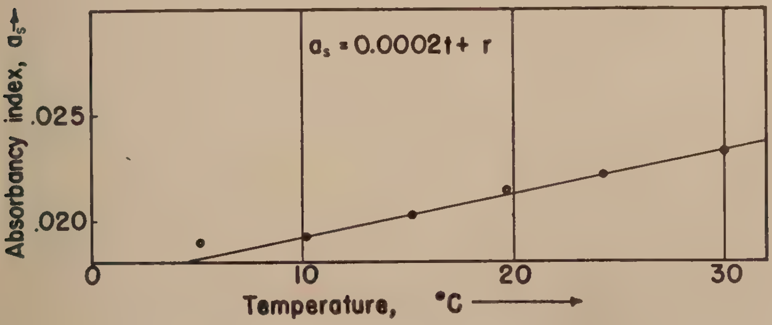

Figure 3. Absorbancy index as a function of temperature.

temperature between 10° and 30° (Figs. 2 and 3). The equation of this function is:

$$a_s = 0.0002\,t + r,$$

where a_s is the absorbancy index, t the temperature in degrees centigrade, and r the residual constant.

Previous workers have found an apparent change of concentration of about 1% per degree temperature difference between the temperature of standards and of unknown samples. Calculations based on the above equation are in agreement with these observations.

If a constant temperature bath is available it is obviously best to bring both standard and unknown samples to the same temperature before analysis. An alternate method is to measure the equilibrium temperature of unknown samples and to apply a temperature correction, using the above equation. In the latter method there is the disadvantage that six hours may be required for samples from deep stations to reach an equilibrium temperature, during which time the phosphate content may change significantly. In a water bath, on the other hand, samples can be brought to temperature in ten minutes or less.

PREPARATION OF REAGENTS

Molybdic Acid: Dilute reagent-grade sulfuric acid with an equal volume of distilled water and cool to room temperature. Mix 3 volumes of this dilute sulfuric acid with 1 volume of molybdate solution containing 10 gm of ammonium molybdate [$(NH_4)_6Mo_7O_{24}\cdot 4H_2O$] per 100 ml distilled water. Molybdic acid solution should be stored in a dark bottle and should not be allowed to come in contact with rubber.

Stannous Chloride: Place 2.1 gm of granular tin metal (reagent grade 20 or 30 mesh) in a small beaker and add 22 ml of reagent-grade hydrochloric acid. After solution is complete, usually in 3–4 hours, dilute to 200 ml with distilled water. Add several pieces of mossy tin and store under paraffin oil.

Standard Phosphate: A stock solution containing 3000 µg at. of added PO_4-P per liter is prepared by diluting 0.408 gm of reagent-grade KH_2PO_4 to 1000 ml with distilled water. Several drops of chloroform are added as a preservative. A working solution, containing 30 µg at. of added PO_4-P per liter, is prepared by diluting 10 ml of the stock solution to 1000 ml with low-phosphate sea water (surface water obtained away from the coast). This low-phosphate sea water ordinarily contains from 0.3 to 0.6 µg at/L of phosphate-phosphorus. It is not essential that these standards contain exactly their nominal phosphate content if subsequent dilutions are made accurately, since, in standardization, the *slope* of the curve, absorbancy *vs* concentration, is required rather than the *absolute value* of absorbancy for each concentration.

METHOD OF ANALYSIS

Measure duplicate 100-ml samples for analysis (see *Notes 1 and 2*), including duplicate 100-ml samples of distilled water for reagent blanks. Bring the samples to a known temperature or measure the temperatures of representative samples. To each sample add 1.0 ml of molybdic acid solution, shake thoroughly, and add 0.2 ml of stannous chloride solution (see *Note 3*). After shaking thoroughly, record time of reagent addition. At least 10 minutes, but not more than 25 minutes, after addition of reagents, measure absorbancy of samples and reagent blanks at 700 mμ in a 10-cm absorption cell (see *Note 4*).

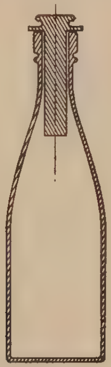

Figure 4. Phosphate sampling bottle. Dimensions of plug depend on volume of bottle used

In order to relate absorbancy to concentration, 3 or 4 standard curves are determined for each batch of reagents. A series of dilutions of standard phosphate solution is made with low-phosphate sea water and these are analyzed as described above. Absorbancy is plotted as a function of concentration and the slope of the curve is determined. The given equation is used to determine the magnitude of the temperature correction. Absorbancy of the reagent blank is subtracted from absorbancy of the sample; the remaining absorbancy is divided by the product of absorbancy index, a_s, and the cell length, l, to give the concentration of phosphate-phosphorus.

Note 1: Smaller samples may be used if a small-volume absorption cell is used, but they must be measured with greater accuracy. If 50-ml samples are used, reagent quantities given should be halved.

Note 2: Samples can be drawn conveniently and accurately in the sampling bottle shown in Fig. 4. The bottle, although it contains a volume somewhat greater than 100 ml, is closed by a loose-fitting brass plug with dimensions such that it will displace sufficient water so that the bottle will deliver 100 ml (precision of about ± 0.5 ml) when the plug is removed.

Note 3: Molybdic acid solution should not be pipetted from a stock reagent bottle because of the danger of contamination. If a buret is used, it must be remembered that molybdic acid solution turns blue on prolonged exposure to light or in contact with rubber. Similarly, stannous chloride solution is readily oxidized when exposed to air. Specially designed reagent dispensers are convenient for precise addition of reagents at sea.

Note 4: Absorption cell windows are gradually stained upon repeated exposure to solutions containing molybdenum-blue. This stain can be removed by filling the cell with a 10% solution of hydrofluoric acid and allowing it to stand for 15 minutes. The extent of this staining and its effect on the absorbancy of samples can be determined by measuring the absorbancy of the cell filled with distilled water, after first balancing the photometer for 100% transmittancy through an air light-path. If such cell checks are made before and after each group of determinations, it is possible to correct for the absorbancy of the cell itself. Then absorbancies of samples can be measured relative to an air light-path rather than relative to a cell filled with water.

RANGE AND ACCURACY OF METHOD

Ayres (1949) showed the value of plotting "absorbtancy" (100 minus transmittancy) against log concentration in studying range and accuracy of a photometric analytical method. He showed, on theoretical grounds, that the straight line portion of this curve reveals the optimum range of the method and that the slope of this line is a measure of the relative analytical error. The optimum range is a function of the wave length used, and the relative error is a function of the concentration of substance being studied.

Such a study of the method described above shows that, when photometric readings are made at 700 mμ in 10-cm absorption cells, the optimum range is from 1.0 to 3.5 μg at. P/L. Although Beers Law seems to obtain down to the very low concentrations, the relative error is greater below 1.0 μg at/L. In a typical curve, shown in Fig. 5, the relative analytical error in the optimum range is 2.8% per 1% photometric error. Between 0.4 and 0.8 μg at/L, however, it is 4.7%. Since the photometric reading error may be reduced to about 0.2%, the relative analytical error becomes only a fifth of these values, or less than 1% in both cases.

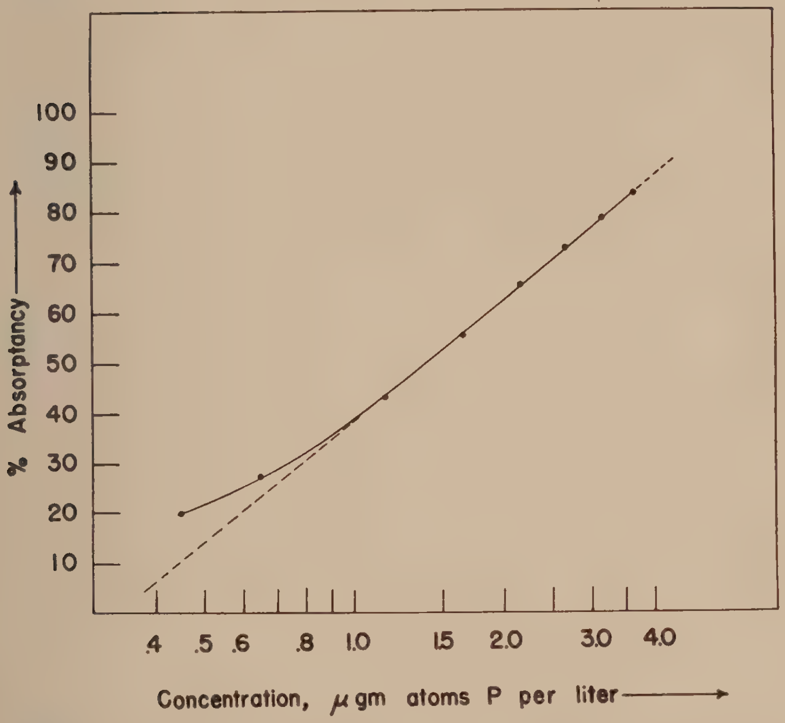

Figure 5. Curve for estimating optimum range and accuracy, according to method of Ayres (1949). Sea water at 10.1°, measured on 10-cm absorption cells at a wave-length of 700 mμ.

There are other important sources of error not treated by Ayres' method. These include sampling errors, error in determining the relation between absorbancy and concentration, and error in determining reagent blank. The presence of certain of these errors, in addition to those inherent in visual colorimetry, makes one question the usual estimates of 5 to 10% accuracy for the traditional method. Although the precision of measurements made by the method described above is usually better than 2% of concentration, the accuracy at the present time cannot be said to exceed 5%.

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Reprinted from COPEIA, 1951, No. 4

CATOSTOMUS ARENARIUS, A GREAT BASIN FISH, SYNONYMIZED WITH *C. TAHOENSIS*.[1]—Our explorations of the freshwater fish faunas of Western North America have indicated that several species now recognized as distinct are invalid. In this note *Catostomus arenarius* Snyder, a nominal species of the Lahontan system, in Nevada and California, is indicated as a synonym of *C. tahoensis* Gill and Jordan.

Catostomus tahoensis Gill and Jordan

In his outstanding treatise on the fishes of the Lahontan system, Snyder (1917, Bull. U. S. Bur. Fish., 35: 47–49) described *Catostomus arenarius* as a new species, on the basis of eight specimens from six localities in the drainage basin of ancient Lake Lahontan. He distinguished *C. arenarius* from *C. tahoensis* by scale number only, giving the range of variation for the lateral-line scales as 68 to 75 for *arenarius* (68 in 1 specimen, 73 to 75 in 7) and as 81 to 96 for *tahoensis*. The paratype that yielded the very low count of 68 has not been relocated. We have failed to confirm such a distinction of a coarse-scaled and a fine-scaled form, for we have recorded a continuous and normal variation of 73 to 100 in specimens from various parts of the Lahontan system, including the available types of *C. arenarius*. The holotype, USNM No. 75654, has 74 or 75; four paratypes, USNM Nos. 21093 and 75679-81, kindly counted for us by E. A. Lachner, have 74 (2) to 75 (2); a fifth specimen 399 mm. in standard length (USNM No. 75245), presumably a paratype (see column 4 of table in Snyder, 1917: 49), has 73 (75 on right side); another paratype, at Stanford University (No. 23949), has about 78. In a series of nearly topotypic specimens in the University of Michigan Museum of Zoology (No. 133840), from the mouth of Truckee River, Nevada, the counts range from 83 to 98. The scale counts on both sides of four topotypes at the University of California, from the east shore of Pyramid Lake near the Pyramid, varied from 86 to 100 (counts kindly made for us by Warren Freihofer, through the courtesy of Paul R. Needham). In 16 specimens from Carson River, 2 miles west of Fallon, Nevada (UMMZ No. 124855), the variation is from 78 to 97.

That two forms are not represented is further indicated by the fact that the coarse-scaled individuals are otherwise indistinguishable from other specimens in the same collections. These individuals certainly appear to be extreme variants of *C. tahoensis*. Their selection by Snyder from the large series available to him and their designation as a distinct species appear attributable to his stated belief and indicated conviction that each major drainage of western United States has a pair of species of *Catostomus*, respectively representing a coarse-scaled and a fine-scaled series. He (Snyder, 1917: 42, footnote *b*) further expressed the view that the *Catostomus* pairs alternate in abundance in the several drainages. Thus in the Lahontan and Klamath systems, the coarse-scaled types (*arenarius* and *snyderi*) he held to be rare, the fine-scaled forms (*tahoensis* and *rimiculus*) abundant, whereas in the Sacramento system the small-scaled *C. microps* is rare and the large-scaled *C. occidentalis* is widespread. *C. snyderi* is now known to be common.

Rather than comprising just two series of cognate species, the several species of *Catostomus* of Western North America are largely allopatric, and they are readily distinguishable on characters other than scale size. In the Sacramento drainage of California and southern Oregon, *C. occidentalis* is the widespread form, *C. microps* a local isolate of Rush Creek evidently not closely related to *occidentalis*. In the Klamath system of Oregon, *C. snyderi* occurs commonly only above Klamath Falls, whereas *C. rimiculus*[2] lives below these falls as well as in Rogue River. In the Columbia River drainage, *C. macrocheilus* and *C. columbianus* (formerly *C. syncheilus*) inhabit the same streams, but have contrasting ecological requirements (Miller and Miller, 1948, Copeia (3): 177–80). In the Colorado River system, *C. insignis* is almost wholly confined to the Gila River basin, whereas the very different *C. latipinnis* is (or was) widespread, and is sharply segregated ecologically from *insignis* where the two occur in the same waters.

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[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 518.

[2] *Castostomus oregonus* Gilbert (1898, Bull. U. S. Fish Comm., 17 (1897): 2) has page priority over *C. rimiculus*, but is a *nomen nudum*. It was obviously based on the same material and was presumably a manuscript name that was elsewhere changed in the original description to *rimiculus*.

In the eastern tributaries of the Gulf of California, *C. sonorensis* Meek is widely distributed, but *C. bernardini* Girard and *C. wigginsi* Herre and Brock evidently are of very local distribution.

The Lahontan system is not the only major drainage of the West that has but a single representative of *Catostomus,* for the Owens River basin of the Death Valley system also contains only one member of this genus. This distinct species (yet to be described) was referred by Snyder (1917, Proc. U. S. Nat. Mus., 54: 202) to *C. arenarius,* since it has about the same scale counts as were attributed to that nominal species In contrast to the great scarcity of specimens corresponding with "*C. arenarius*" in the Lahontan system, the Owens sucker is common and widespread.

The evidence is compelling that *Catostomus arenarius* was based on large-scaled variants of *C. tahoensis:* (1) specimens agreeing with the description of *arenarius* are rare and sporadic in distribution and nowhere comprise a population; (2) the large-scaled variants in the Lahontan system are otherwise indistinguishable from finer-scaled specimens captured simultaneously; (3) the similarly coarse-scaled suckers that do form populations in the Owens River system are specifically separable on the basis of other characters; (4) the reported difference in scale counts is not as great as Snyder indicated and the low scale counts comprise one end of a frequency curve of normal distribution and of not surprisingly wide range; and (5) the two species of *Catostomus* in other drainages are readily separable on more basic features than scale size, a meristic character subject to much individual and geographic variation.—CARL L. HUBBS, *Scripps Institution of Oceanography (University of California), La Jolla, California,* and ROBERT RUSH MILLER, *Museum of Zoology, University of Michigan, Ann Arbor, Michigan.*

Transactions, American Geophysical Union Volume 32, Number 3 June 1951

MASS MOVEMENTS IN SUBMARINE CANYON HEADS

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(Contribution from the Scripps Institution of Oceanography, New Series No. 519)

Abstract--The repetition of sounding profiles along precise ranges at the heads of the submarine canyons in the La Jolla area has given a sequence of depth changes during the past three years. Changes up to a maximum of 21 ft have been observed. Fill and deepening have alternated, but without any seasonal relationship such as occurs on the local beaches as a response to storm waves. The shallow valley heads are shown to shift in position, and at least one new valley with a maximum depth of 16 ft was formed during the period on an undissected slope. These changes have taken place on the sand-covered slopes inside the rock gorges and appear to be explained by sedimentation and landsliding. The latter may be a combination of creep and sudden shifting of sediment. Sufficient material is being moved by these slides to fill the outer gorges in a matter of a few centuries, but the material is certainly being carried out of the gorges, probably going to form the sand layers in the deep outer trough at the mouth of the canyon. The canyon heads are thought to trap a large proportion of the sand that is carried along the shore by currents. This prevents the formation of sand beaches directly down current from the canyons.

Introduction--The mass movement of sediments down the floors of submarine canyons is a phenomenon which is now well established. Cable companies have long been familiar with the slides at points where their cables cross canyons [SHEPARD, 1932], and engineers have had to contend with sudden deepenings at the ends of piers built into the heads of canyons, and with the slumping of jetties built at similar points. Detailed profiles across the shallow canyon heads off the California coast were first made in 1933. Many repetitions have been made since that time, and significant depth changes have been found on many occasions [SHEPARD and EMERY, 1941]. All the earlier work was carried on by wire soundings because echo-sounding devices were not available for the small boats which must be used for operations near shore and large boats are not practical for marine operations that require highly accurate positions. Since 1947 small portable echo-sounding devices have been available for the work at Scripps Institution, and these have been used on launches and amphibious vehicles (Dukws) for investigation of the changes in the canyon heads at La Jolla. The echo soundings are useful only in the shoalest portions of the canyons, largely because at greater depths the walls are so steep that the echoes become uncertain as to source and no consistency can be obtained in repeating runs. The results to date are by no means as complete as could be desired, so that the present is largely a report of progress.

The changing heads of Scripps Canyon

Accuracy of method--In order to find the exact nature of the changes which have taken place, it is of the utmost importance to have a high degree of accuracy in position and depth. There have been far too many reports of depth changes which are probably based on inaccurate positions, poor depth measurements, or faulty echo-sounding records. Some of our earlier records show definite evidence that changes have taken place, but the only thoroughly accurate and detailed information on canyon-head changes has come from the sounding records of the past three years in the two tributaries of Scripps Canyon known as Sumner Branch and South Branch (Fig. 1). Records of comparable accuracy at the head of La Jolla Canyon have shown much less significant changes. The axis slope of the small valleys at the canyon heads is approximately 6° out to 50 ft and 8° from 50 to 70 ft. Beyond, there are precipitous drops into rock-walled gorges. However, the echo-sounding surveys have adequately covered only the inner portions, where gently sloping, sand-covered walls are found.

A series of surveys has been made by echo sounding along 12 lines which cross the axes of the two canyon heads. These lines are rigidly controlled by very sharp ranges provided by the pilings of Scripps Institution pier, a half mile distant, and the peak of a white house a mile from the pier. Under small wave conditions it is easy to run a line keeping within one or two feet of these ranges. Positions along the range are obtained by marking positions on the tape when a series of pre-arranged sextant angles are observed. The accuracy of the method, at least as it

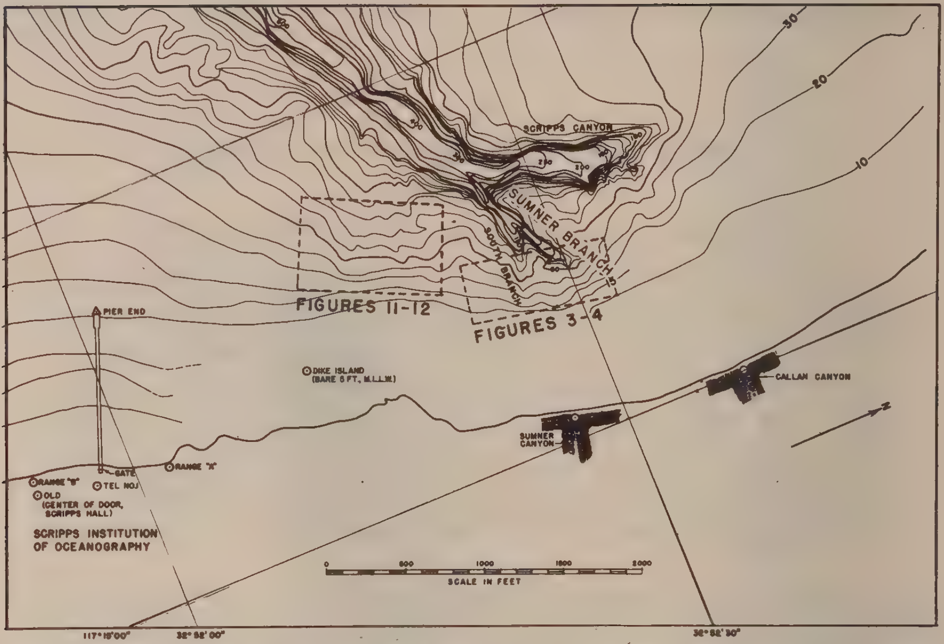


Fig. 1--The head of Scripps Canyon showing the relation of the two tributaries, South and Sumner Branches, to the main canyon; note the shallow valleys inside the rock gorges; changes in these inner valleys form the chief subject of discussion

applies to most of the ranges used in Figures 3 to 9, is indicated by Figure 2, in which two of the fathograms run as repeats on the same day or succeeding day are reproduced. The two outermost ranges are not as easily repeated because of the steep slopes. The records obtained from Scripps Canyon are corrected to the tide gage at the end of Scripps Institution pier so that there can be virtual certainty that no appreciable error comes from the state of the tide. The accuracy of the echo-sounding device is tested by comparing with vertical wire soundings at least twice during each survey. This is particularly important since variation of the frequency may cause errors which would imply depth changes of the order of a few per cent.

When complete checks are used, there can be no reasonable doubt of the existence of major changes such as we have discovered, particularly where they are indicated in a series of ranges.

Nature of changes--Three types of change are observed in the small valleys at canyon heads: one in which the axis depth increases or decreases, a second in which there is a change in the position of the valley axis, and a third in which new valleys develop. The second and third, so far as can be ascertained, are confined to zones where rock outcrops do not exist on the valley walls, but axis depth changes have been definitely established in localities where the canyon walls are rock cliffs.

The nature of the changes in Sumner and South Branches can be illustrated in various ways. Figure 3 gives a series of comparisons showing the progressive changes of contours in these valleys. These charts showed that the valleys under discussion have slight relief. Outward, they either die out or extend into the main branch. Intermediate Branch terminates offshore before extending into the gorge of Sumner Branch, whereas the gully at the head of South Branch is apparently related to the outer gorge. Even the latter is not very stable in position. The net change from January 1948 to February 1950 is shown in Figure 4. It will be noted that the valleys had nearly returned to their previous condition.

In the profiles taken directly from fathograms, comparison is made by superimposing one series on the next as in Figures 5 to 7. The vertical exaggeration in the echo-sounding profiles gives a false impression that actual new significant valleys are formed by some of the depth

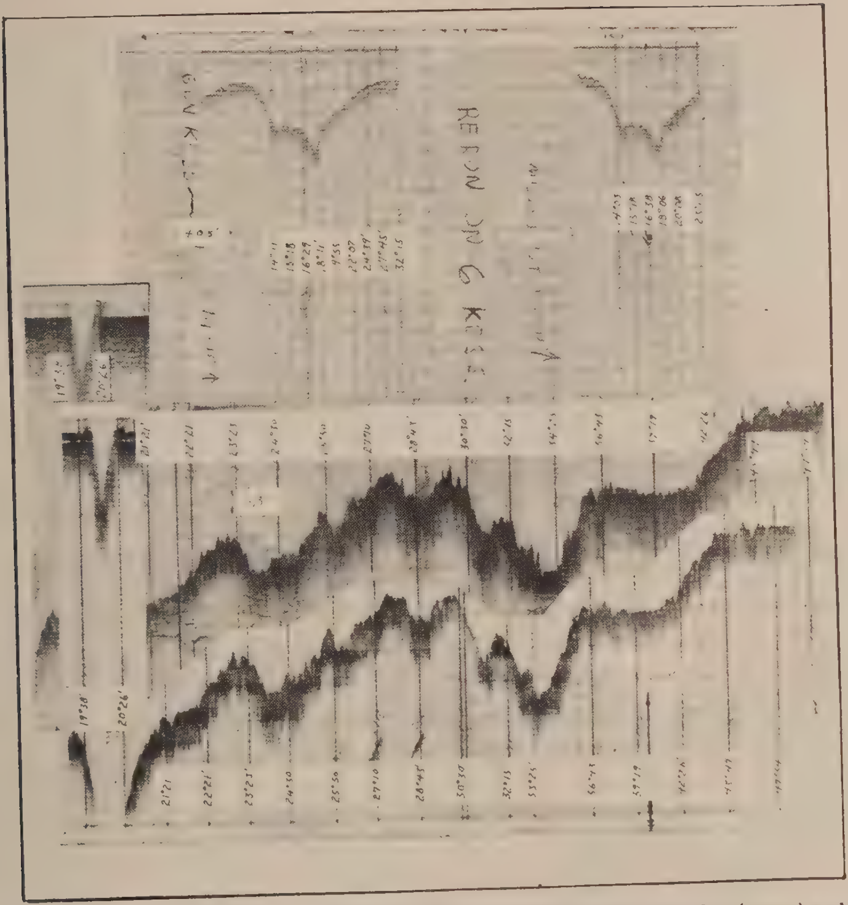


Fig. 2--Comparison of fathograms along the same ranges on the same day (upper) and on two successive days (lower); two different echo-sounding devices were used during the course of the work, accounting for the larger scale on the lower part of the figure; the spikes on the fathogram indicate waves; in judging depths, a line is drawn through these spikes; variations in speed of the boat prevent an exact tracing of one fathogram on top of the other, but the points of reference (given as angles) are for the most part exactly the same; note also that where the fathogram gets too deep for the scale (lower left), a shift can be made onto the next scale

changes. Examination of the accompanying contour maps, however, shows that the new valleys are very small in dimensions and some of them represent a redevelopment of pre-existing valleys.

Another and particularly significant means of comparison is shown in Figures 8 and 9, where the axis depths along each of the sections are plotted against time over the past three years. For South Branch these plottings were easily made since the valley axis could be traced outward continuously into the rock gorge beyond, although at times the inner depression became filled. However, Sumner Branch offered more of a problem since Intermediate Branch, the principal shallow inner gully, is not connected with the outer gorge. As a result, a different valley was used for the outer lines because it seemed advisable to show the changes in both of these features in order to compare the times of change in the different parts of the tributaries (Fig. 10). Examination of the profiles of axis change shows that there has been a series of deepenings occurring contemporaneously along most of the axis of the same branch and at slightly different times in the two branches.

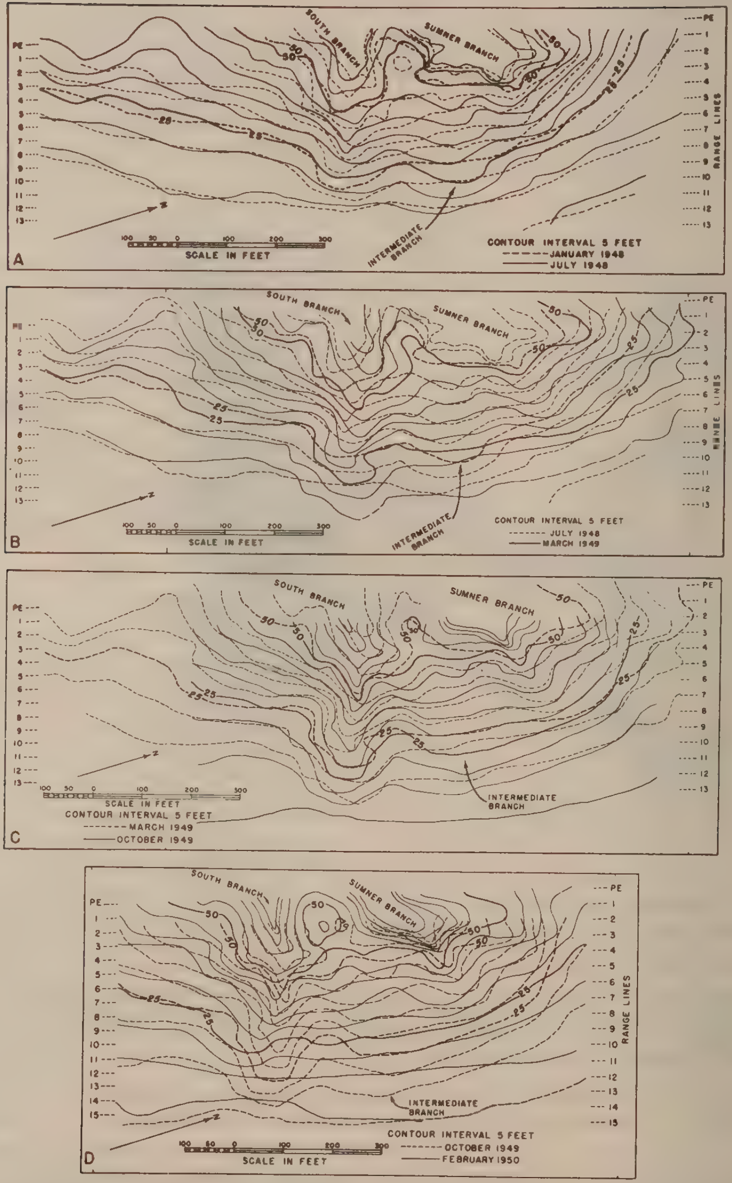

A
SOUTH BRANCH
SUMNER BRANCH
INTERMEDIATE BRANCH
CONTOUR INTERVAL 5 FEET
JANUARY 1948
JULY 1948
SCALE IN FEET
100 50 0 100 200 300
RANGE LINES
PE
1
2
3
4
5
6
7
8
9
10
11
12
13
50
25
Z
B
SOUTH BRANCH
SUMNER BRANCH
INTERMEDIATE BRANCH
CONTOUR INTERVAL 5 FEET
JULY 1948
MARCH 1949
SCALE IN FEET
RANGE LINES
C
SOUTH BRANCH
SUMNER BRANCH
INTERMEDIATE BRANCH
SCALE IN FEET
CONTOUR INTERVAL 5 FEET
MARCH 1949
OCTOBER 1949
D
SOUTH BRANCH
SUMNER BRANCH
INTERMEDIATE BRANCH
CONTOUR INTERVAL 5 FEET
OCTOBER 1949
FEBRUARY 1950
SCALE IN FEET
RANGE LINES
14
15

Fig. 3--Illustrating the changing contours in the shallow valleys at the heads of South and Sumner Branches; note that Intermediate Branch virtually disappears at times, also that at the time of the February 1950 survey South Branch had been filled in for a length of over 200 ft; as will be seen from Figure 8, the branch re-opened in May 1950; the accuracy of these large-scale maps becomes somewhat questionable along the outer lines

The cycles of fill and cut are variable in length in both canyons and certainly not related to the storm season. Both the cut and the fill were progressive during a sequence of surveys. It is

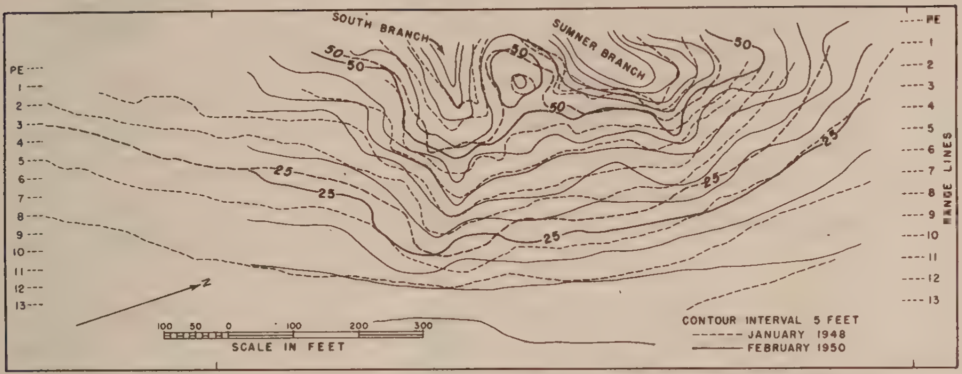


Fig. 4--Contour map showing the total change in contours in 25 months; note that in the February 1950 survey the valley heads have approximately the same depths as the valleys of the earlier survey, but that they are shifted in position

unfortunate that trouble with equipment made it impossible to determine whether or not the alternation of fill and cut which occurred between October 1949 and May 1950 was gradual or whether the changes took place rapidly. Future work with surveys more closely spaced in time is obviously needed.

New Valley development--The formation of a new valley formed somewhat to the south of South Branch deserves especial attention. One line had been run repeatedly across the area where the new valley appeared for almost three years before there was any indication of this valley (Fig. 7, 2 pile range). Subsequently New Valley (Fig. 11) has been completely surveyed and is found to have a maximum depth below the shelf of about 16 ft. The valley dies out in both directions and shows no indication of being connected directly with the rocky canyon outside. It has gentle slopes and is not an impressive feature. The time of valley development seems to have been after an earthquake which shook La Jolla enough to be widely felt, although no damage resulted. The changes in South and Sumner Branches observed after this earthquake were in the nature of fill (Fig. 3D and 7) which, however, may have been entirely independent of the earthquake.

Unfortunately only one line is available to show the changes between October 1949 and February 1950, but older lines are available which cover most of the length of the new valley. These show no sign of a pre-existing valley. It seems likely that the major changes which produced the entire valley took place at more or less the same time. The net changes on the sea floor are given in Figure 12, where contours are based on depth differences between the old and new lines. Examination of these contours or isopleths indicates that the changes represent the removal of material to a maximum depth of slightly over 20 ft along a portion of a slope which had an inclination of approximately four degrees.

Nature of bottom--The character of the bottom material in the changing valley heads inside the gorge is known as the result of considerable sampling as well as from observations during dives. As indicated previously, no rock has been found although the rock walls are closely adjacent to the outermost of the echo-sounding lines. The sediment is almost entirely fine sand but with a trace of silt. The median diameters shown from analyses indicate the sand varies from 0.160 to 0.108 mm, in general decreasing with depth. A maximum of about three per cent silt was found in the deeper samples (about 60 ft deep). The sand on adjacent portions of the shelf is comparable in grain size with the sand in the valleys. In the outer gorge, however, the sand is somewhat finer than on the adjacent shelf, and the silt content runs up as high as 60 per cent in some samples. In the shallow valleys, samples obtained after a fill had approximately the same diameters as those obtained after deepening.

In a considerable number of sampling attempts only eel grass or kelp was recovered. Some of this grass was so decomposed as to have a strong smell of H_2S. In places the sand was crossed by rows of echinoids (sand dollars). Ripple marks were found on the sand, with wave lengths of about three inches. In view of the depth, they are probably related to the surface wave action.

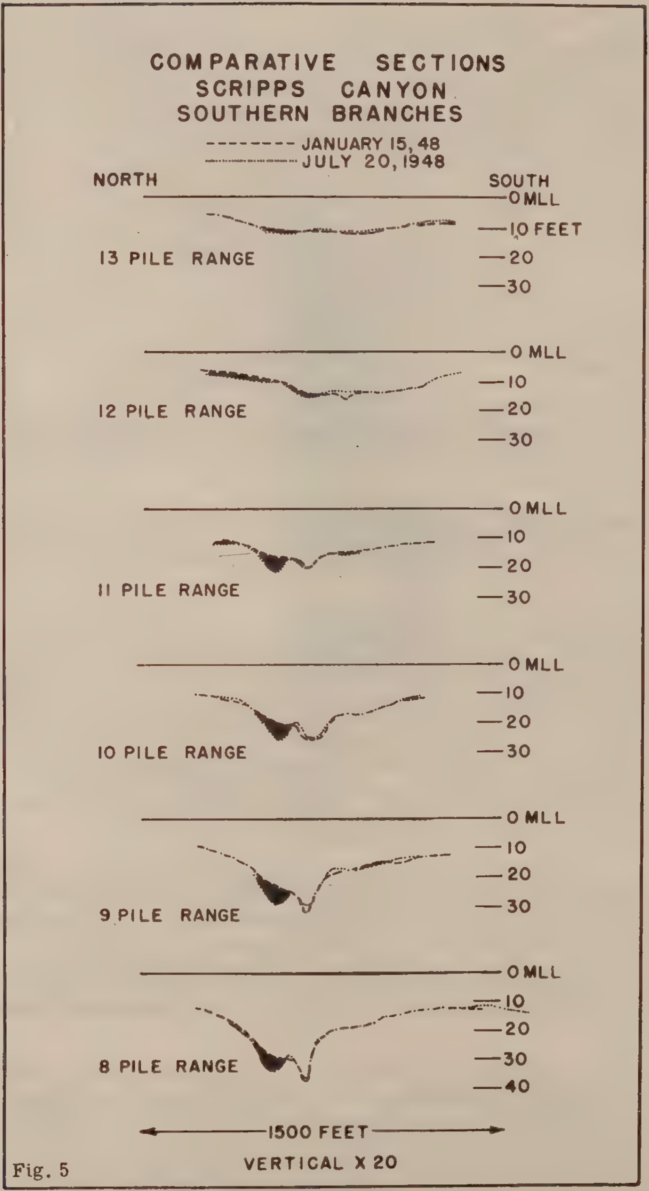


Fig. 5

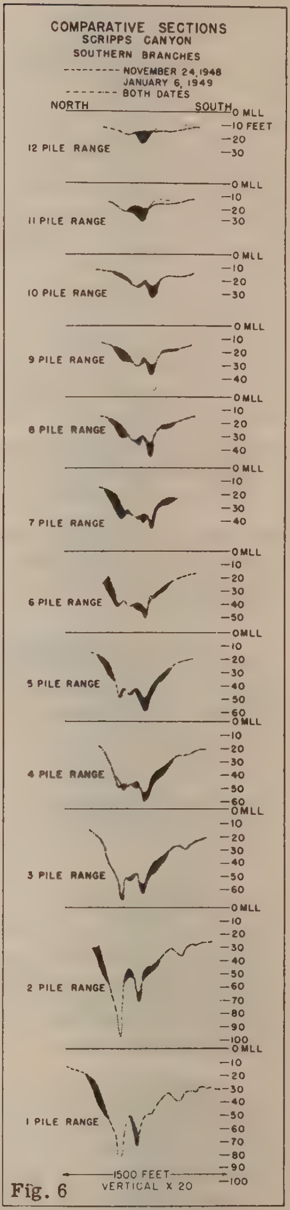


Fig. 6

Fig. 5--Superimposed tracings from fathograms (adjusted to give agreement as to position), illustrating the development of Intermediate Branch (left) between January 1948 and July 1948; the black area shows deepening; note that the right-hand valley (South Branch) was filled somewhat during this same period; it should be borne in mind that these sections show a great vertical exaggeration and comparison should be made with the contour maps to obtain a better idea of the actual slopes involved

Fig. 6--Superimposed tracings from fathograms of November 1948 and January 1949 (adjusted to give agreement as to position); the sections indicate the extension shoreward of the head of South Branch (right) and a considerable removal of material from the sides of Intermediate Branch (12 pile to 9 pile) and of Sumner Branch (8 pile to 5 pile)

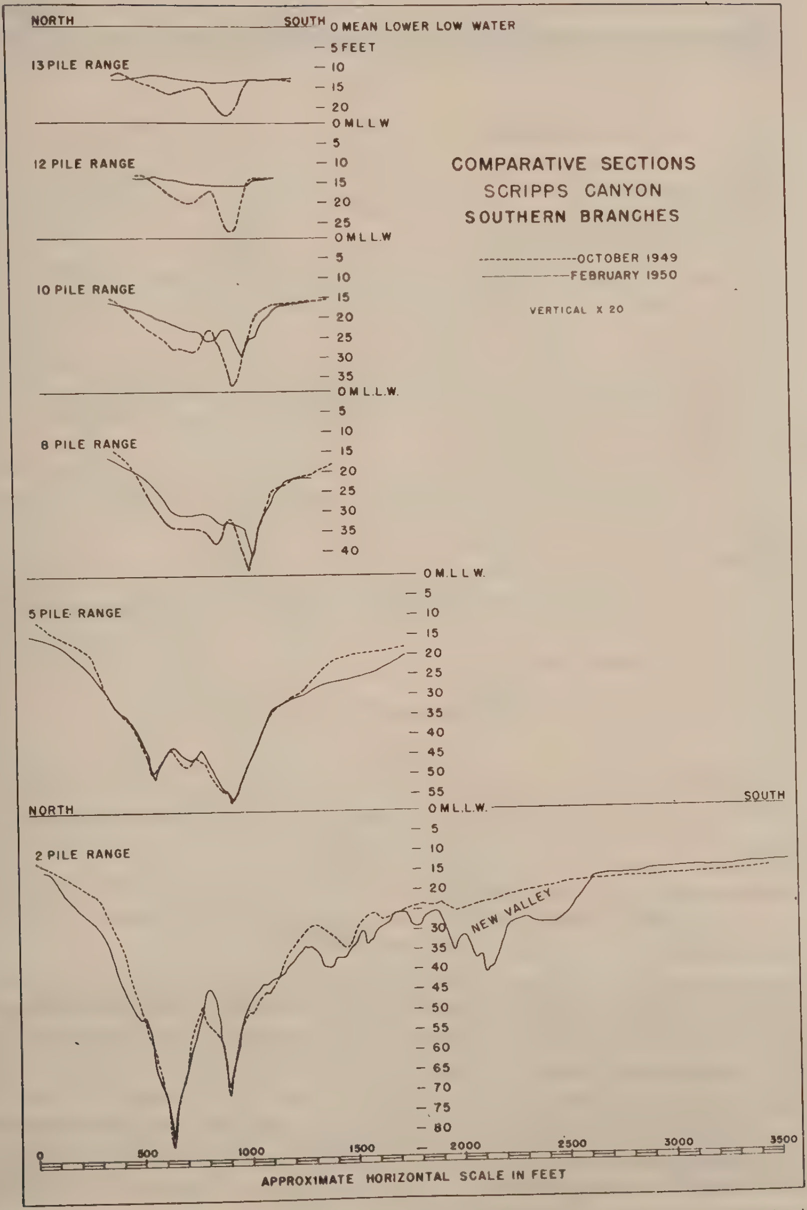


Fig. 7--Superimposed tracings from fathograms (adjusted to give agreement in position); these tracings are from fathograms of larger scale showing more details than those of Figures 5 and 6; note the development of New Valley between the times of these surveys, also the extensive fill in Intermediate and South Branches (see Fig. 3); the decreasing depth of the ridge shown between the two canyons along "2 pile range" is probably authentic although subject to slight uncertainty due to the steepness of the slopes. The authenticity of the development of New Valley is assured since numerous earlier surveys conformed with the October 1949 line and a series of surveys show absolute agreement with February 1950 (see Fig. 2)

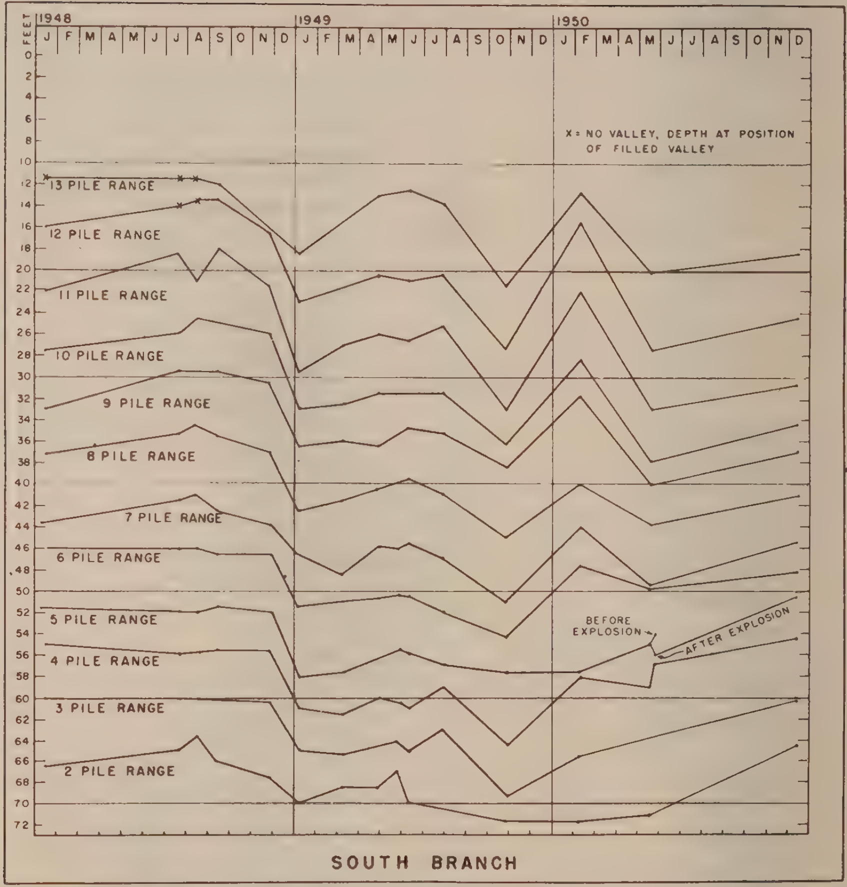


Fig. 8--Showing the sequence of cut and fill in three years of surveys along the head of one valley

Effects of explosives--An attempt was made to produce a deepening of the valley heads in Scripps Canyon by setting off explosives on the bottom. Although charges up to 100 lb were employed, no appreciable depth changes occurred. Local deepening of the order of two feet took place directly under the spot where the explosive had been placed, but the effect seems to have been only that of blowing a small hole in the bottom. Another effect was the boiling-up of sediment to the surface along with decaying eel grass. The rise of similar decomposed eel grass over the canyon axis was observed by a fisherman at another time when there had been no explosive or disturbance of any kind. In this last case the gas which comes from the decay of the eel grass must have been released suddenly, causing a boiling-up of the bottom material which, according to the fisherman's description, was not unlike that which we observed at the time of the explosions.

Amount of displaced sand--The comparative surveys show that in the course of a year a considerable amount of sand is displaced from the slopes inside the canyon heads. If this material moves out along the canyon axis, as seems likely, it would either cause a relatively rapid fill of the outer canyon or, if it is carried beyond, make an appreciable contribution of sand to the floor of San Diego Trough. Thus, for example, measurement by planimeter indicated a loss of 3,500,000 cu ft in the area shown in Figure 12, and nearly 4,000,000 cu ft in all was displaced in the formation of New Valley at the end of 1949, while in the change between February and May 1950 about 300,000 cu ft was moved. Assuming that the former change was exceptionally large, it is still not unlikely that a million cubic feet move out of the Scripps Canyon heads each year. If this is distributed evenly along the outer axis of Scripps Canyon, which extends for about one mile and has a

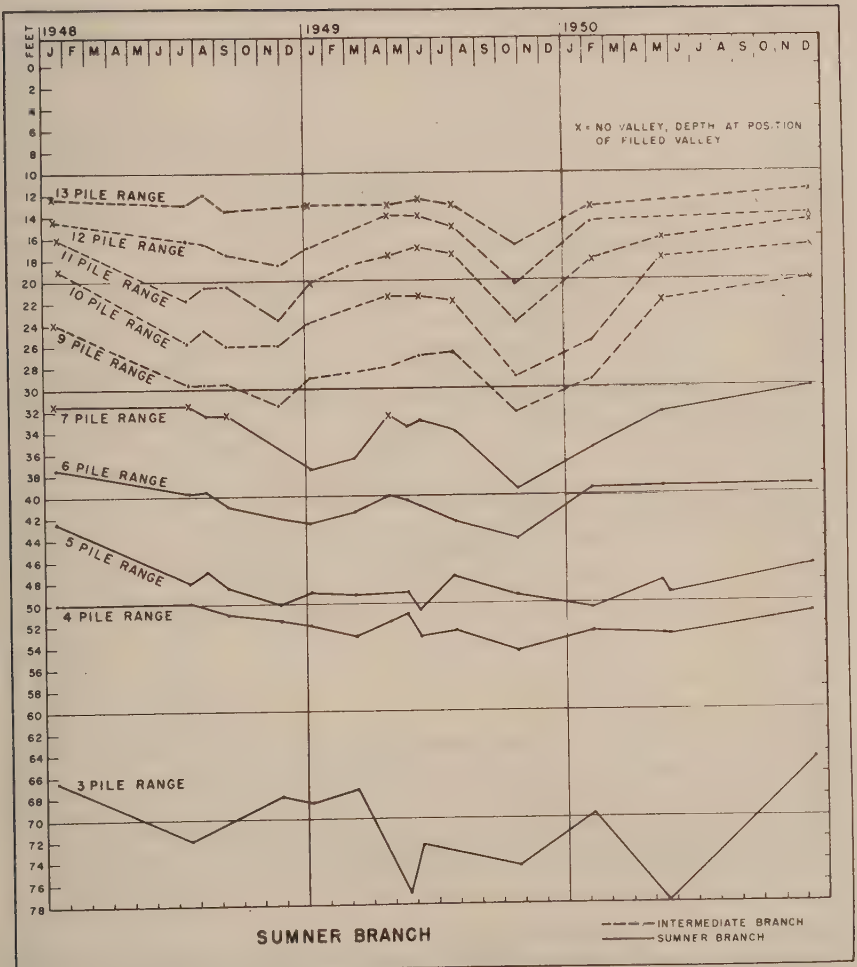


Fig. 9--Showing the same sequence as in Figure 8 for Intermediate Branch (profiles 13 to 9) and Sumner Branch (profiles 7 to 3); note the great increase in gradient indicated by the large interval between the 4th and 3rd pile

floor width of about 50 ft, it would cause an annual fill of the order of four feet. At this rate the canyon would be eliminated in a few centuries. It seems highly probable, however, that much of this displaced material continues beyond the main portion of Scripps Canyon. In fact, the sand layers found abundantly on the floor of San Diego Trough outside La Jolla Canyon [LUDWICK, 1950, and SHEPARD, 1951] can be most easily explained as having moved out of the canyon.

Nature of mass movements

The most obvious explanation for the deepenings in the valley heads is that there are occasional submarine landslides which carry material out into deeper water. Alternatives worth considering are (1) that large waves and their associated currents carry the material down the canyon axes [JOHNSON, 1939], and (2) that turbidity currents are set up by heavily-laden, muddy waters accompanying floods.

The available information suggests that landslides are the explanation and that the alternatives are at most of minor importance. Thus the times of deepening in the branches of Scripps

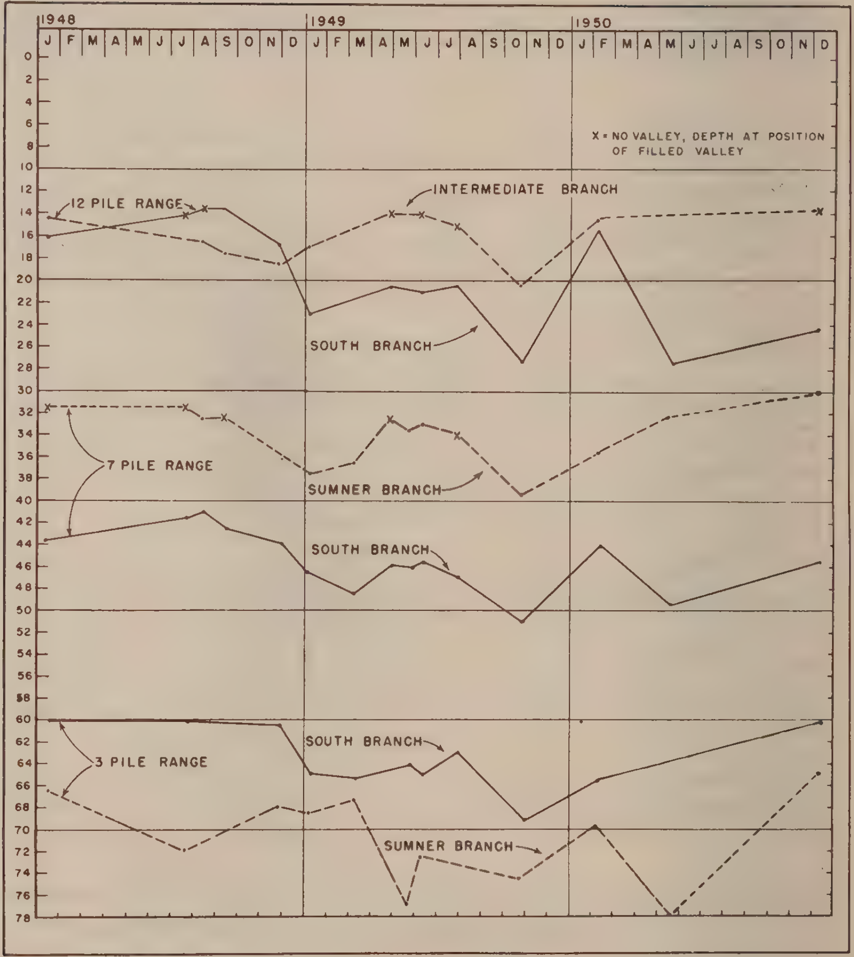


Fig. 10--A comparison of times of change in the heads of South Branch with those in Intermediate and Sumner Branches

Canyon include August to October 1949, a period when there were no unusually large waves nor were there any heavy rains which could have set up turbidity currents. Furthermore, the times of largest waves and most rain, that is, February through April, have been more the times of fill than deepening in the La Jolla Canyons. During the largest flood of recent years, March 1938, a sediment trap was in place on the floor of La Jolla Canyon. Recovery of the trap after the storm showed that no unusual movement had taken place and there was as much sediment on the down canyon as on the up canyon side.

The rapid deepenings of as much as 25 ft at the end of the Redondo City pier, built into the head of Redondo Canyon, are particularly indicative of submarine slides. According to fishermen on the pier, one of the deepenings took place in a period of one-half hour. It occurred at a time when there were relatively small waves and after a period of long-continued fill which had been recorded by the city engineer for a period of about a year. Other pier-end deepenings both at Redondo and at Moss Landing (at the head of Monterey Canyon) have occurred during storm-wave conditions, but the large scale and rapidity of deepening indicate that the storm waves were merely a trigger effect which set off a slide.

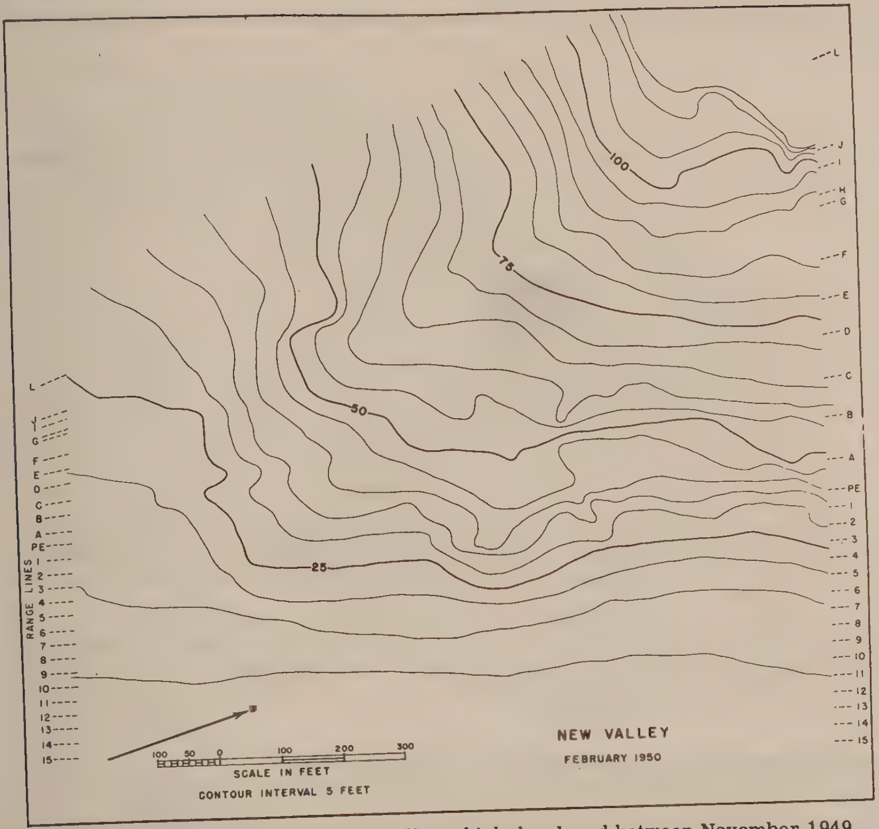


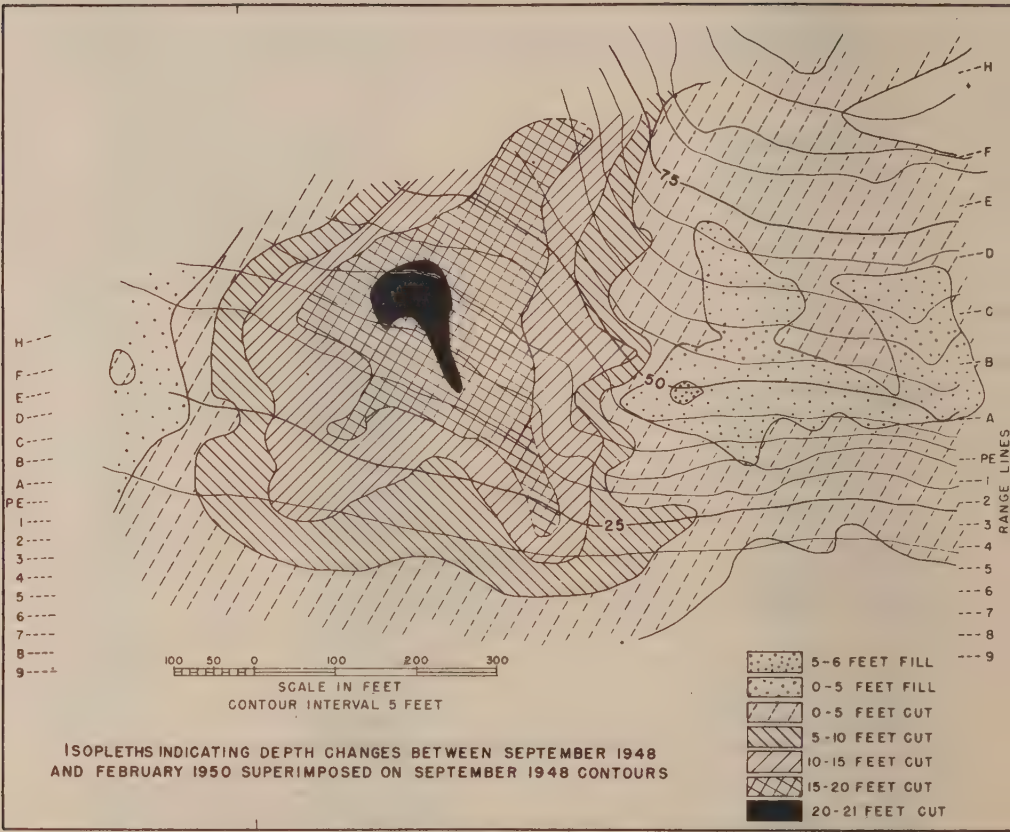
Fig. 11--Showing the shape of New Valley which developed between November 1949 and February 1950 (see also Fig. 12); note that it reaches a maximum in the middle and practically dies out outside as well as inside; it will be seen that this valley is very different from the great rock-walled gorges shown in Figure 1

Theoretically there are no serious difficulties in the assumption that slides of some nature produce the removal of the rapidly accumulating canyon head fill. Mass movements on land are known to occur at angles as low as one degree in mud and of about five degrees in sand (Karl Terzaghi, personal communication). Evidence of slides on the sea floor at angles as low as one degree has been reported [**ARCHANGUELSKI**, 1930]. Since there is some mud deposited along with the sand, the slopes at the canyon heads are sufficiently steep to induce slides even in saturated sediments on land so that they are presumably steep enough for movements on the sea floor where the displaced materials are more buoyant than on land. Furthermore, the inclusion of decaying kelp and eel grass in the sand results in the formation of pockets of gas which must greatly facilitate sliding action.

The evidence of successive deepenings suggests that slow slumping takes place in addition to the rather rapid slides indicated at pier ends. During a dive into Sumner Branch, Frank Haymaker discovered a trench a few inches deep and a few feet wide along the north side of the fill [SHEPARD, 1949, pl. 3, Fig. 2]. This feature may give some clue as to the types of movement which take place. However, until we are able to make daily observations or obtain continuous instrumental records in some of the deeper areas, considerable uncertainty is going to remain relative to the exact nature of these changes.

Significance of canyon head depth changes

The following questions arise as the result of the observed canyon head changes:


H
F
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1
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4
5
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7
8
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RANGE LINES
75
50
25
100 50 0 100 200 300
SCALE IN FEET
CONTOUR INTERVAL 5 FEET
ISOPLETHS INDICATING DEPTH CHANGES BETWEEN SEPTEMBER 1948 AND FEBRUARY 1950 SUPERIMPOSED ON SEPTEMBER 1948 CONTOURS
5-6 FEET FILL
0-5 FEET FILL
0-5 FEET CUT
5-10 FEET CUT
10-15 FEET CUT
15-20 FEET CUT
20-21 FEET CUT

Fig. 12--Showing the magnitude of depth changes involved in the development of New Valley; note that part of the survey is based on soundings in 1948, but at least the major change quite certainly occurred after the October 1949 survey

(1) Does the greater portion of the sand being carried along the coast by longshore currents fall into the canyon heads and become permanently lost to the beaches?
(2) Are the canyon heads becoming slowly filled with sediment despite the occasional deepenings?
(3) Do slides occur with sufficient violence so that canyon floor erosion takes place with the result that the canyons are getting deeper?

Clear-cut answers to these questions are not yet possible, but clues which have come from the investigations may provide partial answers.

Canyon heads as sand traps--The period of three and a half months during which the head of South Branch was filled by as much as four to eight feet shows that a very considerable amount of sand (the type of sediment in the canyon head) must be carried into these valleys where they extend in near shore. This fill took place during a period when there was only a small amount of rain, so that the sediment must have been provided by the longshore transport of sediment by currents related to waves.

The currents associated with canyon heads [SHEPARD and INMAN, 1950] are not conducive to the by-passing of sediment. Commonly sediment is carried out from the shore by rip currents which extend out from the convergence zones on either side of the canyon heads. However, during times of longshore winds the longshore currents tend to flow past canyon heads with much less outward deflection. At La Jolla the coastal zones which are down current from the two canyon heads are virtually free of sand, which indicates that little sand passes the canyon heads. On the

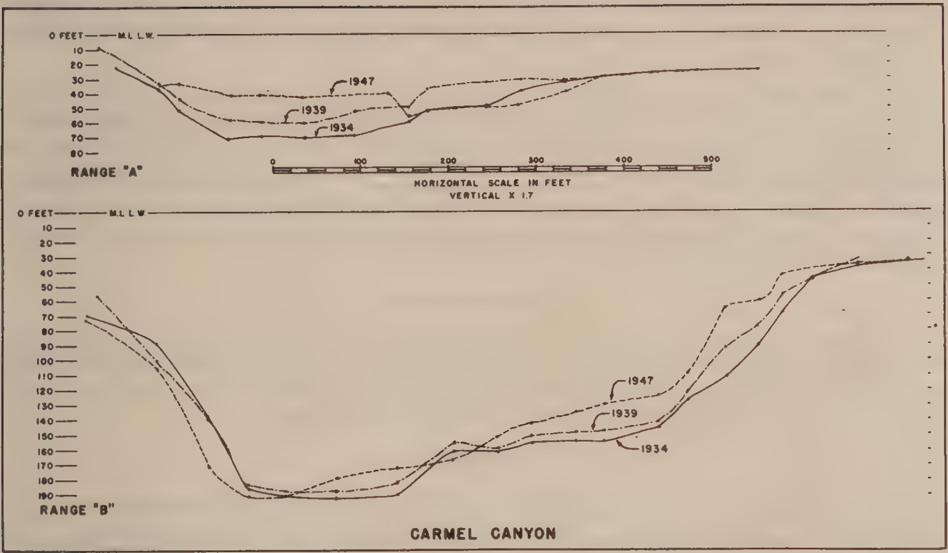

Fig. 13--Showing a series of depth changes over a period of 13 years in the head of Carmel Canyon; an important item of the change consists of a shift of the channels of the canyon head

other hand, the building of jetties at Hueneme, California, resulted in serious sand loss to the shore in a down-current direction, which seems to indicate that prior to the construction at least part of the littoral drift of sand was moving around Point Hueneme past the canyon head [INMAN, 1950]. The jetties apparently deflected this sand supply into the canyon so that it was no longer available for the down-current beaches.

It is possible that sediment dropped into submarine canyon heads can be returned to the beaches provided the slope is relatively gentle. The placing of a sediment trap in the very head of La Jolla Canyon above the zone of steep slope resulted in obtaining more sediment on the down canyon side than up canyon. However, this one case may not be very representative. It would certainly be surprising if sediment is moved up the five- to eight-degree slopes of the heads of Scripps Canyon and of course virtually impossible that sediment could move up the precipitous slopes which lead into the rock gorge. Material falling into these gorges must move down canyon since otherwise it would soon fill the canyons. As we have seen, even the inner slopes are ample for slides.

Net results of canyon head changes--The evidence regarding the ultimate fate of submarine canyons, provided conditions remain as at present, is by no means conclusive. The oldest soundings along good ranges across canyon axes date back to 1934. They are mostly in water deeper than that which has been discussed. Also, the interval may not be long enough to find any net change, but the changes may be considered for what they are worth. In Scripps Canyon a good range shows a depth of 483 ft in 1934 and 471 at the same place in 1948. In La Jolla Canyon, also on a good range, the depth in 1937 was 188 as compared with 184 in 1947. In Carmel Canyon (Fig. 13) the greatest depth in 1934 along a good range was 193 ft compared with 192 in 1947, while on another range it varied from 72 to 56 ft. All of these comparisons indicate a slight net shoaling, but the changes, some of which are scarcely outside the limits of operational errors, are no greater than the alternating changes at shoaler depths clearly demonstrated in the valleys at the head of Scripps Canyon. A change over a period of five years in Newport Canyon indicates slight deepening. Over longer periods we have the testimony of surveys dating back 60 years or more at certain canyon heads in California. However, because of paucity of soundings, all one can conclude from these older surveys is that there has probably been no appreciable landward extension of the canyon heads. Except where up-current breakwaters have trapped sand supplies, the beaches inside canyons show little change from the condition they had 50 years ago. Piers inside canyons are still located at the same place although some of them have undergone periodic slides as indicated previously.

Thus the evidence to date is that canyons are not undergoing any appreciable net changes. Sediment introduced at the heads eventually slides out along the axis. Whether the movement outside the steep heads continues as a slide or is in the nature of a turbidity current is not yet known, but the movement of sand over very low slopes is suggestive of turbidity current transport [SHEPARD, 1951].

The cores obtained along the axis of La Jolla Canyon indicate that material may be very slowly filling the canyon, since there are various layers of coarse sediment interbedded with muddy materials. If the slides were scouring out the canyons completely and even cutting away the underlying rock, one would expect to find only thin layers of fine sediment overlying rock floors rather than the alternating layers shown in the cores. In the East Coast canyons, cores suggest that deposition has been going on at least as far back as the last glacial stages--since cold water planktonic Foraminifera are found underlying the temperate water Foraminifera of the upper sediments [PHLEGER, 1942].

Acknowledgments

Very able assistance in various phases of this work has been given the writer by Ruth Young, Douglas Inman, Don Sayner, David Poole, and George Brayton. The drafting was done by Don Sayner. This work represents in part research carried out for the Office of Naval Research and the Beach Erosion Board under contracts with the University of California.

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(Communicated paper received December 29, 1950;
open for formal discussion until November 1, 1951.)

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Identification of cyprinid fish reported from Kansas as Squalius elongatus

Identification of cyprinid fish reported from Kansas as *Squalius elongatus*[1]

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Among the most puzzling records of freshwater fishes from eastern North America is that of *Squalius elongatus* from Kansas (Hay, 1887: 249). Suspecting that the record was based either on a misidentification or on an intergeneric hybrid, rather than on an example of *Clinostomus elongatus* (Kirtland), we have not included Kansas in the range of the species (Hubbs and Lagler, 1941: 56; 1947: 64). Since, however, this dace has a markedly localized and disjunct distribution, especially toward the west, and since several northern types range or once ranged southward as far as the Missouri River system in Kansas, the record, though from a stream far removed from others known to be occupied by the species, has not totally lacked plausibility. W. Ralph Taylor on examining the specimen in 1949 determined that it has the pharyngeal teeth alignable in 3 rows, as in most Old-World cyprinids but as in no native North American species. Since this observation accentuated the enigma, I studied the specimen (U.S.N.M. 38233) critically, with the cooperation of Leonard P. Schultz, on January 13, 1951. It was reported by Hay (*l.c.*) as having been collected by him in the North Fork of Solomon River at Lenora, Kansas, in July, 1885.

The 48-mm. specimen, though now very soft and partly covered with white scum, retains characters adequate for identification. Despite its dentition, it clearly represents no known Old-World species, and there appears to be no good reason to doubt the indicated provenance.

Though it is possible to count the teeth on the one remaining (left) arch as in 3 series (2, 2 or 3, 5), their arrangement and form stamp the dentition as abnormal. Enumerated from above, the second tooth of the main (structurally innermost) row is rather loose, as though it were a replacement, and is somewhat curved spirally over the tooth at its outer side, which is small and might be aligned either in the main row, or, as I have done, in the second row. The third tooth of the main row is greatly and irregularly swollen, is slightly out of line, and bears at its base, fused with it, what appears to be the trace of an old tooth. The tip of this large tooth is hooked outward and upward, so as to surround partly

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[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 520.

the small tooth standing beside the second tooth of the main row. What can be regarded as the middle row comprises the remnant fused to the base of the enlarged third tooth of the main row, the small tooth which might also be aligned in the main row, and, uppermost and outermost, a still smaller tooth that might be aligned in the outer row. The third or outer row, on the assumption that the teeth are triserial, comprises 2 small teeth, corresponding to the normal second or outer row of American cyprinids with biserial teeth. It would seem that the replacement teeth had become anchylosed to the arch, abnormally, while the teeth which should have been replaced remained. Abnormally seriated pharyngeal teeth have occasionally been observed in other American cyprinids, for example in an *Acrocheilus alutaceum* × *Ptychocheilus oregonense* hybrid (Hubbs and Schultz, 1931: 5). An occasional abnormal increase in the number of pharyngeal teeth was noted by Hay (1887: 251) for *Hybognathus nuchalis* and other species. Such an increase, he inferred, may have been responsible for his earlier proposal of *Tirodon* for a specimen of *H. nuchalis* with extra teeth. In synonymizing *Tirodon amnigenius* with *H. n. nuchalis* (Hubbs, 1947: 175-176), I overlooked this inference.

Since the pharyngeal dentition is abnormal and since no American cyprinid has triserial teeth, the identification is pointed toward a species with biserial teeth. No approach is shown toward *Clinostomus elongatus,* which has the lower jaw sharply projecting, the upper lip very narrow across the midline, the dorsal fin rather posteriorly inserted, the body compressed, and the lateral band very diffuse. The specimen shows too little approach toward *Clinostomus* in any of these characters to warrant it being considered even as a hybrid involving *Clinostomus elongatus* as one parental species. This is a point that definitely called for consideration, since *Clinostomus* on approaching local extirpation is especially apt to hybridize with other genera (Greene, 1933: 87-89; Hubbs, 1951: 452). The possibility of its being a *Chrosomus* × *Clinostomus* hybrid is further excluded by the rudimentary development and the low number, approximately 7, of the gill-rakers and by the simple S-loop of the intestine.

Another unusual character of the specimen is the number, 9, of dorsal rays, rarely shown by any minnow of eastern North America other than the very dissimilar *Opsopoeodus emiliae* Hay. The anal has 8 rays, as does each pelvic.

Disregarding by reason of their abnormality the dentition and the dorsal rays, the characters of the specimen prove to those of *Semotilus atromaculatus atromaculatus* (Mitchill). It is true that no barbel can be found, but the concealed and almost rudimentary barbel is often absent in *Semotilus* and was reported to be so in a specimen of the same series recorded by Hay (1887: 249) as *Semotilus*. The scales number about 69 in the lateral line and about 47 before the dorsal, as in *S. a. atromaculatus*, and have the proper structure. Also characteristic of *Semotilus* are the large mouth (upper jaw about 2.6 in head), with moderately oblique gape rising to about level with middle of eye; the slightly included lower jaw; the moderate expansion of the upper lip at the midline; the narrow, even-edged lateral band (faintly retained), ending before a round, black basicaudal spot; the trace of pigment remaining on the dorsal fin near front of base; the small eye (4.5 in head to bony opercular margin); the little compressed body; the slender, scarcely compressed head (depth about 2.0 in length); the small dorsal fin (depressed length 2.0 in distance forward to occiput), originating midway between the caudal base and the middle of the eye.

It is concluded that the record of *Squalius elongatus* from Kansas was based on a specimen of *Semotilus atromaculatus atromaculatus* with abnormal dentition and with an unusual number (9) of dorsal rays. All other species appear to be excluded from consideration in the identification of the specimen even as a possible hybrid with the *Semotilus*.

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Reprinted from JOURNAL OF BACTERIOLOGY
Vol. 62, No. 1, July, 1951
Printed in U.S.A.

HYDROGEN UTILIZATION BY SOME MARINE SULFATE-REDUCING BACTERIA[1]

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Received for publication April 24, 1951

Sulfate-reducing bacteria which oxidize molecular hydrogen have been detected in water or soil by various workers (Starkey and Wight, 1945, ZoBell, 1947). Sisler and ZoBell (1950) found such bacteria to be widely distributed in marine sediments, where they are believed to be important geochemical agents. Pure cultures proved to be species of *Desulfovibrio*, some of which are capable of an autotrophic existence in mineral solutions with molecular hydrogen serving as the sole source of energy.

The autotrophic activity of H_2-oxidizing sulfate reducers was first demonstrated by Wight and Starkey (1945) and confirmed by Butlin and Adams (1947). The enzyme which activates H_2 was designated hydrogenase by Stephenson and Stickland (1931*a*,*b*). The part played by H_2-consuming *Desulfovibrio* species in the anaerobic corrosion of iron has been discussed by Starkey and Wight (1943, 1945).

This paper is concerned with a study of the physiology of several cultures of *Desulfovibrio* isolated from marine sediments, with particular reference to their hydrogenase activity under various conditions.

MATERIALS AND METHODS

Heterotrophic sulfate reducers were tested for their ability to utilize H_2 in screw-capped test tubes of semisolid lactate agar containing inverted vials filled with H_2 (figure 3, Sisler and ZoBell, 1950). Inoculated tubes were incubated at 28 C along with sterile tubes of similar medium containing vials of H_2, which served as controls. Lactate medium having the following composition was used for this purpose:

Calcium lactate	3.5 g	Dibasic potassium phosphate	0.2 g
Neopeptone	1.0 g	Ferrous ammonium sulfate	0.1 g
Yeast extract	1.0 g	Agar	3.0 g
Ascorbic acid	0.1 g	Sea water	750.0 ml
Magnesium sulfate	0.2 g	Distilled water	250.0 ml

The ascorbic acid helped to maintain reducing conditions (Kligler and Guggenheim, 1938) essential for the initiation of growth of sulfate reducers. In inorganic media employed for the growth of autotrophs, sodium sulfide was substituted for the ascorbic acid to create reducing conditions. Once the sulfate reducers start to grow, they produce enough H_2S to provide a reducing environment. The reaction of the sulfide with ferrous iron blackens the medium to a degree that is roughly proportional to the amount of sulfate reduced. The pH of the medium was 7.5 following autoclave sterilization.

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[1] Contribution from the Scripps Institution of Oceanography, New Series No. 521. This paper is a contribution from the American Petroleum Institute Research Project 43A.

For studying autotrophic sulfate reducers a similar mineral medium, free of organic matter, was dispensed in pairs of glass-stoppered bottles connected with a siphon in such a way that the utilization of H_2 in the inoculated bottle resulted in a like volume of medium being siphoned over from the reservoir bottle (figure 1, Sisler and ZoBell, 1950). At the termination of the experiment the residual gas in the inoculated bottle was analyzed by a Fisher unitized precision model Orsat apparatus (Matuszak, 1934) or by mass spectrometer, the latter determinations being made by the Richfield Oil Corporation, Wilmington, California.

Cell suspensions for chemical analysis and for use in Warburg respirometer experiments were grown in 20-liter lots of mineral salts solution over-layered with H_2 purified by passage through alkaline pyrogallol solution and sterile cotton. The cells were harvested with a Sharples supercentrifuge.

Enrichment cultures of sulfate reducers were purified by preparing serial dilutions for inoculating nutrient agar deeps. From the highest dilution showing growth of sulfate reducers, further serial dilutions (1:10, 1:100, etc.) were used to inoculate tubes of nutrient agar which, in the molten state, was drawn into sterile tubes of 2 mm inside diameter and 60 cm long. After the agar had solidified, the ends of the tubes were coated with sterile paraffin, and the tubes were incubated at 28 C. Tubes showing typical black discrete colonies were selected for the isolation of pure cultures. By breaking the tube near such colonies, they could be transferred aseptically with an inoculating needle to appropriate media or to dilution water. Microscopic examination and cultural tests established the purity of the isolated cultures.

EXPERIMENTAL RESULTS

Hydrogenase activity of sulfate reducers. Out of a total of 39 cultures of sulfate reducers isolated from marine sediments, 33 exhibited hydrogenase activity after 9 weeks' incubation at 28 C as indicated by their ability to utilize H_2 in lactate medium. Although there was evidence of growth and H_2S formation by all cultures after 1 week's incubation, only a few consumed detectable quantities of H_2 during this period. The rate at which heterotrophic sulfate-reducing bacteria consumed H_2 is illustrated by data summarized in table 1.

Some cultures exhibited hydrogenase activity only after 20 to 24 weeks' incubation at 28 C in nutrient medium enriched with H_2, which suggests that hydrogenase may be an adaptive enzyme. Our results indicate that not all strains of sulfate-reducing bacteria utilize H_2, some cultures having been maintained for several months in the presence of H_2 without exhibiting any hydrogenase activity.

A few cultures have been observed that utilize H_2 only in the absence of lactate or other organic hydrogen donors, but such obligate autotrophs are in the minority. Eleven of the 39 cultures tested utilized H_2 in purely inorganic medium; of these only 3 failed to utilize H_2 in lactate medium.

Many anaerobes found in marine sediments besides sulfate reducers consumed H_2 in nutrient medium containing lactate, peptone, and other organic compounds or their decomposition products, presumably with the reduction of carbon compounds (ZoBell, 1947). Among the possible hydrogen acceptors of such cultures are CO_2 and other one-carbon-atom compounds known to be reduced to methane (Barker, 1943; Kluyver and Schnellen, 1947; Stephenson and Stickland, 1933) and various organic or amino acids (Farkas and Fischer, 1947; Farkas and Schneidmesser, 1947; Hoogerheide and Kocholaty, 1938; Lascelles and Still, 1946). To date, however, the only substances found to serve as hydrogen acceptors for pure cultures of sulfate-reducing bacteria are sulfate, sulfite, thiosulfate, sulfur, CO_2 or carbonate, certain unsaturated organic acids, and nitrogen.

TABLE 1

Average amount of H_2 consumed after different periods of incubation at 28 C by duplicate cultures of sulfate-reducing bacteria in tubes containing 20 ml of semisolid lactate agar and 2.5 ml of H_2

CULTURE NUMBER	H_2 CONSUMED AFTER			
	1 week	4 weeks	7 weeks	9 weeks
	ml	*ml*	*ml*	*ml*
29:57-1	0.4	2.1	2.5	2.5
29:65-128	0.0	0.0	0.0	0.0
29:66-26A	0.0	0.4	0.6	1.4
29:66-27	0.4	2.5	2.5	2.5
29:129-5	0.0	0.2	1.7	2.1
29:130-2	0.0	0.0	0.2	0.9
29:130-4	0.2	2.3	2.5	2.5
29:136-1	0.2	1.9	2.3	2.5
29:136-4	0.0	0.0	0.4	1.6
29:136-9	0.0	0.2	0.9	1.4
29:193-7	0.3	1.7	2.0	2.5
None (control)	0.0	0.0	0.0	0.0

CO_2 reduction by autotrophic sulfate reducers. Evidence has been obtained for the reduction of CO_2 by sulfate-reducing bacteria by cultivating pure cultures for several serial transfers in mineral salts solution. The growth or multiplication of the bacteria resulted in an accumulation of organic metabolic products in amounts that were proportional to the decrease in the total CO_2 content of the medium. Moreover, the quantity of H_2 consumed was more than the amount required to account for the amount of H_2S formed from the reduction of sulfate, the latter requiring 4 volumes of H_2 for each volume of H_2S produced:

$$H_2SO_4 + 4H_2 \rightarrow H_2S + 4H_2O$$

Whereas the H_2/H_2S ratio approximated 4 for "resting" cells in sulfate medium containing no CO_2, the H_2/H_2S ratio ranged roughly from 5 to 10 for most actively growing cultures of sulfate-reducing bacteria. If sulfate is reduced only to free sulfur, as has been claimed for certain cultures by Datta (1946), or if it is reduced to some product intermediate between sulfate and sulfur, as postulated by Baars (1930), the H_2/H_2S ratio would be less than 4. The representative results summarized in table 2 were obtained by incubating cultures in 100 ml of mineral salts solution overlayered with 100 ml of H_2 in glass-stoppered bottles. The volumes of residual gases, including total CO_2, calculated at standard conditions, were determined at the termination of the experiment.

The $(H_2\text{-}H_2^s)/CO_2$ ratios given as the last column in table 2 are especially significant. These values represent the amount of H_2 available for the reduction of CO_2 after subtracting the amount of H_2 required (indicated by H_2^s) to account for the H_2S produced. Assuming that H_2 is utilized for the reduction of either sulfate or CO_2, the only substances in the medium capable of being reduced, and assuming that the CO_2 is reduced only to a primary building block of bacterial cell substance represented by (CH_2O), the theoretical $(H_2\text{-}H_2^s)/CO_2$ ratio would be 2:

TABLE 2

H_2 consumed, H_2S produced, and CO_2 reduced in 100 ml of purely mineral medium by cultures of autotrophic sulfate-reducing bacteria in 3 weeks at 28 C

BOTTLE NUMBER	CULTURE NUMBER	H_2 CONSUMED	H_2S PRODUCED	CO_2 REDUCED	H_2/H_2S RATIO	$(H_2\text{-}H_2^s)/CO_2$ RATIO
		ml	*ml*	*ml*		
1	43:70-12	23.8	2.2	4.6	10.8	3.3
2	43:70-12	18.5	1.7	3.3	10.9	3.5
3	43:74-54	9.1	1.7	0.8	5.3	2.9
4	43:74-54	9.3	1.7	1.0	5.5	2.5
5	43:74-58	33.1	4.5	6.6	7.4	2.3
6	43:74-58	29.9	3.9	6.4	7.7	2.2
7	43:74-71	34.7	4.8	5.0	7.2	3.1
8	43:74-71	34.5	5.0	4.6	6.9	3.2
9	None (control)	0	0	0		
10	None (control)	0	0	0		

H_2^s = H_2 required to account for H_2S formed.

$$CO_2 + 2H_2 \rightarrow (CH_2O) + H_2O$$

However, all cultures gave $(H_2\text{-}H_2^s)/CO_2$ ratios exceeding 2, which suggests that substances more reduced than (CH_2O) were formed. Such substances have proved to consist at least in part of lipids and hydrocarbons. There is considerable variation in the competition for H_2 by sulfate and CO_2 among different cultures as indicated by the ratios in the last two columns in table 2, and also considerable variation was found in the amounts and kinds of reduced carbon compounds produced by H_2-consuming sulfate reducers.

Products of autotrophic metabolism. The formation of methane by a small percentage of our cultures of H_2-consuming sulfate reducers, which appeared by the usual criteria to be pure, was indicated by Orsat analyses and confirmed by mass spectrometer examination of residual gases.

Mass spectrometer analyses also helped to establish that hydrogenase-producing sulfate reducers may, after prolonged incubation, bring about the quantitative removal of H_2 from media containing an excess of sulfate or carbonate. Culture 48:43, for example, removed the last detectable trace of H_2 from 100 ml of mineral medium to which 100 ml of H_2 had been added, during five weeks' incubation at 28 C while producing, among other reduction products, 0.7 ml of methane.

The small amount of methane produced by autotrophic sulfate reducers (table 3) shows that methane formation is only an incidental and not the principal part of their metabolism. In fact, the cultures recorded in table 3 are the only ones among 39 studied to date which have been found to produce any methane.

During 50 days' incubation at 32 C in 15 liters of mineral medium, culture no. 45:10-12 consumed 13,416 ml of H_2, the volume being corrected for standard conditions. The good agreement between the amount of H_2S produced, namely 1,032 ml, and the amount of sulfate reduced, 4.92 g, indicates that this culture reduced sulfate almost completely to H_2S, the theoretical amount of H_2S that could be produced from the complete reduction of 4.92 g of sulfate being 1,123 ml. An H_2/H_2S ratio of 13 (13,416/1,032) shows that something besides sulfate was reduced, and indeed it was found that a total of 3,910 ml of CO_2 (carbonate, bicarbonate, and CO_2 all calculated as CO_2) had disappeared from the system.

TABLE 3

Methane detected by mass spectrometer in cultures of sulfate-reducing bacteria after 3 weeks' incubation at 28 C in 100 ml of mineral medium enriched with H_2

CULTURE NUMBER	H_2 CONSUMED	H_2S PRODUCED	CH_4 PRODUCED
	ml	*ml*	*ml*
43:0-13	28.4	3.1	0.3
43:0-99	42.7	5.8	0.6
43:100-109	36.5	4.0	0.3
43:101-105	19.8	1.8	0.2
43:103-102	43.1	6.4	1.4
48:43	24.0	2.4	0.2
None (control)	0.0	0.0	0.0

Although no gaseous hydrocarbons were produced by culture no. 43:10-12, in the experiment described in the preceding paragraph, 0.72 g of CCl_4-soluble material was extracted from the bacterial cell substance that developed in 16 liters of medium. Of this, 0.21 g proved to be an oily unsaponifiable material consisting largely of combined hydrogen and carbon. This could account for the $(H_2\text{-}H_2^s)/CO_2$ ratio of 2.37.

The remarkably high lipid yield is of special interest. The heat of combustion of 0.72 g of bacterial lipids is 6,830 cal, assuming that it is comparable to animal and vegetable oils having an average heat of combustion of 9,500 cal per g (Hodgman, 1947). Combustion of 13,416 ml of H_2 to water yields 40,700 cal. Thus 17 per cent of the energy of the H_2 oxidized by the autotrophic sulfate reducer could be accounted for as energy stored as lipids.

Spectroscopists, working under the supervision of Dr. L. M. Henderson of The Pure Oil Company, Crystal Lake, Illinois, who examined an aliquot of the unsaponifiable material produced by the autotrophic sulfate reducer reported that, "The infrared spectrums of the sample furnish partial, but not complete, evidence that the compounds present in the sample are composed for the most part of saturated $—CH_2—$ groups with possibly some $C—CH_3$ groups. No other groups were evidenced. This would indicate that the compounds present are paraffinic or naphthenic hydrocarbons." The infrared spectrums showed no evidence for the presence of C—O, C=O, or O—H linkages, but the sample was not large enough to establish that these linkages were not present in very small percentage amounts.

TABLE 4

Results of growing sulfate reducer no. 45:117 for 45 days at 32 C in 16 liters of mineral salts solution overlayered with H_2

Total amount of H_2 consumed (standard conditions)	19,500 ml
Total amount of CO_2 consumed (including carbonates)	4,110 ml
Total amount of H_2S produced (standard conditions)	2,155 ml
Ratio of H_2/H_2S (19,500/2,155)	9.1
Ratio of $(H_2—H_2^s)/CO_2$ (19,500-8,620/4,110)	2.6
Terminal pH of medium (from initial pH 7.7)	8.4
Terminal E_h of medium (from initial E_h near 0)	−310 mv
Weight of cell substance recovered (dry basis)	3.67 g
Weight of CCl_4-soluble fraction	0.75 g
Weight of unsaponifiable material	0.148 g

It is not to be concluded from these and similar observations that autotrophic sulfate reducers produce crude oil, although traces of oily, CCl_4-soluble, unsaponifiable compounds, definitely more reduced than (CH_2O), are produced as part of the bacterial cell substance. The production of paraffinic hydrocarbons by heterotrophic cultures of sulfate-reducing bacteria was reported by Jankowski and ZoBell (1944), and the observations of Oakwood (1944) suggest the rather common synthesis of hydrocarbons by micro-organisms as part of their cell substance.

Table 4 summarizes the results of an experiment similar to that previously described. The CCl_4-soluble unsaponifiable material produced by H_2-consuming sulfate reducers growing in inorganic medium had a consistency and appearance of amber colored grease. Spectroscopic examinations indicated that at least part of it consisted of paraffinic or naphthenic hydrocarbons.

The ability of autotrophic sulfate reducers to utilize CO_2 as the sole hydrogen acceptor was demonstrated by growing cultures for several generations (seriatim transfers) in mineral salts solution containing less sulfate than one part per million (calculated from impurities in reagents used to prepare medium). Neither growth nor H_2 uptake, however, was nearly as rapid in sulfate-free media as in similar media enriched with sulfate (table 5). In order to minimize the amount of sulfate carried into the medium in the first transfer, washed cells were used, which may account for activity slower than that in the second and subsequent transfers. There was no evidence for the cultures becoming acclimatized to sulfate-free medium nor did they lose their ability to reduce sulfate. When transferred back into sulfate medium, the cultures produced H_2S vigorously.

Hydrogenase activity by "resting" cells. Washed cells suspended in mineral solution in Warburg microrespirometer flasks were found to utilize sulfate almost exclusive of CO_2 or carbonate as hydrogen acceptor. Cells of H_2-consuming sulfate reducers were harvested by centrifugation and then washed repeatedly in phosphate-saline buffer solution containing a trace of sodium sulfide to maintain reducing conditions essential for the stability of hydrogenase. The washed cells were placed in the respirometer flasks with magnesium sulfate or sodium bicarbonate solution to serve as hydrogen acceptor in one of the side arms of the flask. Filter papers soaked with KOH were placed in alternate flasks for H_2S absorption. The flasks were agitated for 15 minutes while flushing pure H_2 through the system. The manometers were closed while filled with H_2 and then equilibrated. After further agitation, the sulfate or bicarbonate solution was tipped into the flasks containing the washed cells, and the flasks were again agitated. Periodic readings were taken to determine change in volumes from which the amount of H_2 consumed and H_2S produced was calculated.

TABLE 5

H_2 consumed and H_2S produced by culture 43:11 in 2 weeks at 28 C per liter of mineral media containing sulfate or carbonate

HISTORY OF CULTURE	CO_2 OR CARBONATE ONLY		CARBONATE PLUS SULFATE	
	H_2 consumed	H_2S produced	H_2 consumed	H_2S produced
	ml	*ml*	*ml*	*ml*
First transfer	1	0.0	46	4.1
Second transfer	12	0.0	106	11.3
Third transfer	14	0.0	87	12.0
(Sterile control)	0	0.0	0	0.0

In systems to which no carbonate had been added, it was found that the endogenous metabolism of the washed cells resulted in the liberation of a little CO_2. This observation, coupled with finding no H_2 uptake in the absence of sulfate or other hydrogen acceptor, indicated that CO_2 is not readily reduced by "resting" cells of sulfate reducers. The H_2/H_2S ratios of most cultures of autotrophic sulfate reducers approximated the theoretical value of 4 for sulfate, 3 for sulfite, and 2.5 for thiosulfate (table 6).

Warburg microrespirometer experiments confirmed tests with actively growing cultures that H_2-consuming sulfate reducers utilize sulfite and thiosulfate more readily than sulfate. The sodium salts of these substances were used in the experiments summarized by the data in table 6. Elementary sulfur failed to serve as an hydrogen acceptor in the Warburg experiments, although we have confirmed the observations of Baars (1930) that certain actively growing cultures of heterotrophic sulfate reducers reduce free sulfur.

Washed cells of sulfate reducers with H_2 in Warburg flasks were found to reduce fumarate considerably more rapidly than sulfate. Fumarate is believed to be reduced to acetic acid:

$$\mathrm{HC{-}COOH{=}CH{-}COOH} + 2\mathrm{H_2} \rightarrow 2\mathrm{CH_3COOH}$$

H_2 consumption by cultures of hydrogenase-producing sulfate reducers, growing in media enriched with either linolenic or linoleic acid as the only hydrogen acceptor, indicated that both of these unsaturated fatty acids were reduced, but we have not yet confirmed the reduction of these substances with "resting" cell technique.

TABLE 6

H_2 consumed and H_2S produced at 30 C per hour per mg (dry basis) of washed cells of sulfate reducers in microrespirometers containing different hydrogen acceptors

LOT	CULTURE NUMBER	HYDROGEN ACCEPTOR	H_2 CONSUMED	H_2S PRODUCED	H_2/H_2S
			mm^3	mm^3	
A	41:38	Sulfate	3.4	0.9	3.8
A	41:38	Carbonate	0.0	0.0	—
A	41:38	Sulfate + Carbonate	4.1	0.9	4.5
B	43:76	Sulfate	8.5	2.4	3.5
B	43:76	Carbonate	0.0	0.0	—
B	43:76	Sulfate + Carbonate	7.9	2.0	3.9
C	43:38	Sulfate	10.6	2.5	4.2
C	43:38	Sulfite	22.8	7.4	3.1
C	43:38	Thiosulfate	20.7	7.8	2.6
D	41:76	Sulfate	6.5	1.5	4.3
D	41:76	Sulfite	17.8	5.4	3.3
D	41:76	Thiosulfate	14.2	5.2	2.7
E	43:6	Sulfate	13.0	3.1	4.2
E	43:6	Fumarate	29.4	0.0	—
F	43:63	Sulfate	8.7	2.1	4.1
F	43:63	Fumarate	12.3	0.0	—

Nitrogen fixation by sulfate reducers. The reduction or fixation of nitrogen by hydrogenase-producing sulfate reducers has been reported by Sisler and ZoBell (1951) in which inverted vials were filled with N_2 to serve as controls alongside vials filled with H_2; a diminution in the volume of N_2 was observed in inoculated media. For this reason helium was adopted for routine use as the inert gas in controls because its volume remained constant except in so far as its solubility was influenced by temperature or pressure changes. Mass spectrometer analyses established that N_2 actually disappeared along with the consumption of H_2 by sulfate-reducing bacteria.

Mass spectrometer data also showed that the ratio of N_2 to argon in gas mixtures decreased under the influence of H_2-consuming sulfate reducers. Since the N_2/A ratio for the atmosphere is fairly constant, any decrease in the ratio in a biological system is suggestive of nitrogen fixation.

Although calling for confirmation by conventional Kjeldahl procedures, these observations on the disappearance of N_2 in cultures of hydrogenase-producing sulfate reducers assume some significance in the light of the recently expressed belief of Lindstrom *et al.* (1949, 1950) that all hydrogenase-producing bacteria can fix nitrogen.

ACKNOWLEDGMENTS

Valuable technical assistance in some of these experiments was given by J. Q. Heplar, Margaret D. Knight, Nance Fountain, and Rose Marie Cassady. Suggestions and constructive criticisms from Professor D. L. Fox have been helpful. The authors also acknowledge with thanks help on analytical problems from W. E. Hanson, L. M. Henderson, L. C. Kemp, Jr., and other members of the Chemical Advisory Committee of the American Petroleum Institute. The mass spectrometer analyses were made by the Research and Development Departments of the Richfield Oil Corporation, The Pure Oil Company, and The Texas Company.

SUMMARY AND CONCLUSIONS

Most of the pure cultures of sulfate-reducing bacteria isolated from marine sediments produce hydrogenase as indicated by their ability to utilize H_2, 33 out of 39 cultures tested showing this ability in lactate medium. Eleven of them multiplied and consumed H_2 as the sole source of energy in purely inorganic medium. A few cultures developed the ability to utilize H_2 after being cultivated in its presence for several generations, which suggests that hydrogenase may be an adaptive enzyme for *Desulfovibrio* species.

The ratio of H_2 consumed to H_2S produced approximated the theoretical value of 4 for the reduction of sulfate by "resting" cells, but greatly exceeded 4 in cultures growing in inorganic medium, thereby proving the reduction of something besides sulfate. The reduction of CO_2 was established both by a decrease in the CO_2 content of inorganic medium and also by the synthesis of bacterial cell substances. An appreciable part of the latter was more reduced than (CH_2O) as indicated by $(H_2\text{-}H_2^s)/CO_2$ ratios exceeding 2, H_2^s being the quantity of H_2 required to account for the H_2S formed.

Up to 30 per cent of the bacterial cell substance was CCl_4-soluble, of which fraction 10 to 20 per cent, or up to 3 to 6 per cent of the cell substance, was an oily unsaponifiable material, probably consisting at least in part of paraffinic or naphthenic hydrocarbons. Traces of methane were produced by 6 pure cultures of autotrophic sulfate reducers.

Warburg microrespirometer experiments with "resting" cells confirmed cultural tests that *Desulfovibrio* species consume H_2 more readily in the presence of sulfite or thiosulfate than sulfate. Fumarate was likewise more readily reduced than sulfate.

The loss of N_2 from cultures, as well as observed decreases in the nitrogen/argon ratio demonstrated by mass spectrometer analyses, indicates that certain hydrogenase-producing bacteria fix nitrogen.

The ability of certain sulfate-reducing bacteria found in marine sediments to consume H_2 may help to account for the general absence of H_2 in natural gases.

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PROCEEDINGS

OF THE

CALIFORNIA ACADEMY OF SCIENCES

Fourth Series

Vol. XXVII, No. 6, pp. 159-176 July 30, 1951

RELATIONSHIPS OF THE PELAGIC SHARK EUPROTOMICRUS BISPINATUS, WITH DESCRIPTION OF A SPECIMEN FROM OFF CALIFORNIA*

BY

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On the night of November 19, 1948, while fishing with a dip-net under a surface light at 34° 57′ N. Lat., 131° 30′ W. Long. (nearly 500 nautical miles off the nearest point of the California coast), in a region where the ocean depths are indicated as ranging between 2,400 and 2,800 fathoms, the junior author and Robert P. Huffer captured a pelagic shark (plates 4–6) that was cruising slowly at the surface. Its small size, slender and cylindrical form, subconic head, round and unprotected eyes, scarcely upturned caudal axis, smooth contours, very slimy skin, almost uniformly blackish color, except on the clear outer parts of the fins, and its very small gill slits gave it an appearance that was distinctly unlike that of most sharks and that was somewhat suggestive, superficially of course, of a lamprey.

We owe thanks to Dr. Léon Bertin of the Muséum d'Histoire Naturelle, Paris, for measurements of the type specimen of *Scymnus bispinatus* Quoy and Gaimard, and to William C. Schroeder of the Museum of Comparative Zoology of Harvard University and W. I. Follett of the California Academy of Sciences for assistance in processing literature.

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* Contributions from the Scripps Institution of Oceanography, New Series, No. 522. Manuscript received December, 1950.

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Identification of Specimen and Status of the Genera Euprotomicrus and Squaliolus

On study the specimen (California Academy of Sciences, No. 20431), a female 233 mm. in total length, is identified with *Euprotomicrus* Gill, a squaloid genus referable to the family Dalatiidae (Scymnorhinidae) as currently recognized. It is clearly conspecific with the hitherto unique type of *E. hyalinus* Eigenmann (1893: 35), which was also collected in the open Pacific between Hawaii and California, but nearer Hawaii. That specimen was destroyed in the San Francisco fire. The one at hand is the only extant example of the genus known from the Pacific Ocean and, so far as we know, the only one in an American museum.

It seems highly probable that *E. hyalinus* is identical with *E. bispinatus* (Quoy and Gaimard). Garman (1913: 235) doubted its distinction and Fowler (1941: 265) synonymized it with that species. The obviously pelagic habitat of *E. bispinatus* and the wide temperature difference between its known areas of occurrence suggest that it is a widely ranging species. In addition to the two known localities in the northeastern Pacific, the record stations for *E. bispinatus* comprise the islands of Mauritius (Île de France) and Bourbon (Réunion) in the Indian Ocean and Campbell Island, far south of New Zealand (see synonymy by Fowler). The New Zealand record (references in Phillipps, 1927: 10) seems to have been in error, according to evidence later presented by Phillipps (1928: 224–225).

The new specimen does differ in certain respects from the only generally available recent description of *E. bispinatus*, namely Fowler's. Though this author attributed his redescription to Quoy and Gaimard (1824: 197, pl. 44, figs. 1–2), an examination of the original description shows that Fowler must have based his account, including measurements, largely on the rather crude figure (which was reproduced in outline by Phillipps, 1928, fig. 5), and must have used methods of measurement different from those we adopt.

Fowler's indication that the pectoral extends half way to the first dorsal in the type was obviously drawn from the main figure, which must be in error. That this fin in the type as well as in our specimen extends less than one-third the distance to the origin of the first dorsal is indicated by the size of the fin shown in the ventral view in the type figure, by measurement of a topotype given by Müller and Henle (1841: 95) and, conclusively, by remeasurements of the holotype made for us by an assistant to Dr. Léon Bertin in accordance with our specifications.

Confusion was also encountered in regard to the position of the first dorsal fin, but again the full evidence fails to confirm suggestions of a specific difference. In his purported restatement of the original description, Fowler wrote "first dorsal inserted midway between snout tip and caudal base'' (which would indicate an approach toward *Squaliolus),* but the figure shows the position midway between snout tip and the end of the caudal fin. Our specimen has the fin inserted even farther back, midway between the tip of the caudal and the middle of the eye. Duméril (1865 : 457), who had three specimens, indicated the dorsal origin as ''située un peu en arrière de la première moitié de la longueur totale.'' Fortunately, the type is extant. Dr. Bertin's measurements (p. 170) indicate that the origin of the dorsal in the type is essentially as in our specimen. He has also compared a copy of our figures with the holotype of *E. bispinatus,* and concurs in the view that *E. hyalinus* is probably a synonym of *E. bispinatus.* Accepting this view, we treat *Euprotomicrus,* like most related genera, as monotypic.

Garman (1913 : 234), Bigelow and Schroeder (1948 : 500), and Fowler (1941 : 264) synonymized *Squaliolus* with *Euprotomicrus,* but in our opinion the generic separation is fully justified, even in a conservative concept of the genus. *Euprotomicrus* differs from *Squaliolus,* as described by Smith and Radcliffe *(in* Smith, 1912 : 683–685, fig. 4, pls. 50 and 54), in the following respects:

(1) The total lack of the first dorsal spine. To forestall any thought that the name *bispinatus* suggests dorsal spines in the type species of *Euprotomicrus,* we point out that this name obviously was derived from the spiny process on each pelvic fin of the male holotype.

(2) The more posterior origin of the first dorsal fin, which is much nearer the insertion of the pelvic than that of the pectoral fin, rather than the reverse, and is well behind instead of well before the middle of the total length.

(3) The more reduced size of the first dorsal fin. The base of this fin is less than one-thirtieth, instead of more than one-twentieth, the total length.

(4) The less excessively elongated second dorsal base, which is less than one-fourth, instead of nearly one-half, the interspace between the origins of the paired fins. The dorsal base does not overlap the pelvic base, as it does in *Squaliolus.*

(5) The rounded rather than pointed caudal lobes.

(6) The thickly rounded rather than pointed snout, in both side and top views.

(7) The smaller head. The head length is about one-fifth rather than one-third the total length.

(8) The longer mouth grooves, in lateral projection about two-thirds rather than one-third the preoral length.

(9) Probably also in dentition: the upper teeth are arranged more in quincunx than in the straight rows that were figured for *Squaliolus* and the lower teeth have the crowns in full contact basally, instead of being separated by the outer shoulders of the bases, as figured. Each of these

shoulders, in consequence, lies wholly on the base of the next outer tooth.

A third species, *Squaliolus sarmenti* de Noronha (1926), from Madeira, has been referred to *Euprotomicrus* (Maul, 1949: 139), but obviously should be retained in *Squaliolus*. In fact, there seems to be no valid ground for separating *S. sarmenti* from the Philippine species *S. laticaudus*. The first dorsal fin was indicated as being somewhat more posterior, but on comparing the photographs and considering the distortion of the preserved specimens, we fail to appreciate the distinction. Consequently, we synonymize *S. sarmenti* with *S. laticaudus* and thus reduce *Squaliolus*, as well as *Euprotomicrus*, to monotypic status.

That *Euprotomicrus* and *Squaliolus* should be treated as monotypic, along with most of the related genera as currently recognized, need not cause concern to a conservative systematist. When species differ so trenchantly from one another, their degree of differentiation is better expressed by full generic separation than by forcing them into larger genera.

RELATIONSHIPS OF EUPROTOMICRUS

Euprotomicrus differs rather sharply from the other genera currently assigned to the Dalatiidae (Bigelow and Schroeder, 1948: 500). It contrasts with *Isistius* in having no subterminal notch in the caudal fin *(Isistius* has a shallow notch at the end of the body axis); the bases of the first dorsal and pelvic fins well separated vertically; the second dorsal basally elongated; the lower teeth strongly oblique instead of erect, with a deep incision on the outer edge and a broad shoulder wholly overlapping the next tooth outward; the dermal denticles more scattered and with roots extending out from the four corners. From *Dalatias* it differs in having the caudal axis much abbreviated and straight rather than upturned; the subterminal caudal notch obsolete, instead of well developed; the first dorsal fin behind instead of before the middle of the total length; the second dorsal fin with a much elongated base, not overlapping that of the pelvic fin; the lower teeth smooth-edged and strongly oblique; the dermal denticles quadrate and hollow-centered, without a posterior spine and without lengthwise ridges. From *Heteroscymnus (longus)*, as described by Tanaka (1912: 102–105, pl. 26), it differs in fin structure in the same way that it differs from *Dalatias*, and further, in that the pectoral fins are rounded; the dentition, however, is similar; further differences are the conically rounded instead of depressed snout and the very large instead of small spiracles. From *Somniosus* it differs in approximately the same fin characters that separate it from *Dalatias*, and in having a much larger spiracle and many fewer teeth, of different form: the upper ones are more needle-like and the lower ones are much less strongly oblique; it differs further in having the center of the denticles pit-like instead of being elevated, with a posterior point.

From *Heteroscymnoides,* as described by Fowler (1934: 239, fig. 4; 1941: 273, fig. 10), it is separable by the form of the caudal fin, which has a horizontal axis and the epaxial part rather more instead of distinctly less expansive than the hypaxial part, and in having the second dorsal fin lower and longer on the base (in the structure of both these fins *Heteroscymnoides* is intermediate between the primitive forms *Dalatias, Heteroscymnus,* and *Somniosus,* and the more specialized *Isistius, Euprotomicrus,* and *Squaliolus). Euprotomicrus* further differs from *Heteroscymnoides* in the posterior displacement of the first dorsal fin, the much shorter and transversely rounded rather than depressed snout, the pitted instead of keeled and spiny denticles.

The characters of the diverse genera that have constituted the Dalatiidae suggest two main phyletic lines, corresponding with the main divisions of the accompanying analytical key, but the interpretation cannot be regarded as certain. The generic characters further suggest, by no means uniquely, a complicated phylogeny, in which similar features in different genera must have evolved independently. Thus the lower teeth presumably changed from erect to oblique in each of the two main groups. Primitive and specialized features are complexly associated in different combinations in the several genera—a common if not usual situation. No simple evolutionary tree (or "bush") can be reliably constructed on the basis of the available evidence. The apparent course of differentiation varies in accordance with the character on which attention is focused and there appears to be no securely objective basis on which to choose between the characters to be emphasized.

In the current classifications, reflected in Bigelow and Schroeder's treatment (1948), the presence or absence of spines in the dorsal fins is given prime and, we think, undue weight. The Squalidae and the Dalatiidae are separated almost solely on this basis. The virtual lack of other diagnostic characters and the strong indications that the spines have undergone obsolescence in more than one phyletic line render the family distinction seemingly artificial and unnatural. In some genera classed in the Squalidae, such as *Centroscymnus,* the dorsal spines are much reduced. Complete obsolescence of the spines would render *Centroscymnus* scarcely separable from *Somniosus,* a large and sluggish shark that might be expected to have lost this armature. Other genera referred to the Squalidae and the Dalatiidae are rather similarly paired, suggesting the multiple origin of the nominal group Dalatiidae. Further evidence on the unnaturalness of the Dalatiidae as currently defined is furnished by *Squaliolus,* which though classed in the Dalatiidae and by some even synonymized with *Euprotomicrus,* retains the first dorsal spine. *Squaliolus* seems to be a terminal element on a phyletic line quite different from that which seems to have led from *Centroscymnus* to *Somniosus* (see generic analysis). It would be extremely difficult to imagine the origin of all "Dalatiidae" from either *Somniosus* or *Squaliolus*. For these reasons it is suggested that the Dalatiidae be fused with Squalidae. Echinorhinidae, then, should likewise be synonymized with Squalidae. Pending thorough morphological studies and a general revision of the squaloids, the two groups thus demoted from family rank may perhaps be retained tentatively as subfamilies, Dalatiinae and Echinorhininae.

That *Euprotomicrus* is a highly modified terminal product of specialization is indicated by the characters that give this genus such an unusual appearance (p. 161), and by the transverse mouth, with very long lateral grooves; the great modification of the teeth, with extreme dimorphism in the two jaws; the peculiar, pitted, quadrate denticles; the great vertical expansion of the upper caudal lobe and the marked abbreviation of the lower lobe; and the greatly reduced number of vertebrae.

OUTLINE OF RELATIONSHIPS

- 1a
  - 2a *(Dalatias)*
  - 2b
    - 3a *(Heteroscymnus)*
    - 3b *(Somniosus)*
- 1b
  - 4a *(Isistius)*
  - 4b
    - 5a *(Heteroscymnoides)*
    - 5b
      - 6a *(Squaliolus)*
      - 6b *(Euprotomicrus)*

ANALYTICAL KEY TO THE KNOWN GENERA OF DALATIINAE

1.

a. Caudal axis strongly upturned; epaxial part of caudal fin little expanded; subterminal caudal notch strongly developed. Mouth more arched and lateral grooves shorter and shallower. Spiracle small. Larger, about 30 cm. at birth and commonly longer than 1 meter as adult. Chiefly in boreal and temperate seas; probably largely demersal.......... 2

b. Caudal axis scarcely upturned or (in *Heteroscymnoides*) weakly upturned; epaxial part of caudal fin much expanded (moderately so in *Heteroscymnoides*); subterminal notch in caudal fin obsolescent (weak in *Isistius*). Mouth essentially transverse; lateral grooves very long and deep. Spiracle large. Small size, unknown over 50 cm., and most specimens well under 30 cm. Chiefly in warm seas; probably largely pelagic.......... 4

2.(1a)

a. Lower teeth erect and serrate.......... *Dalatias*

b. Lower teeth directed outward and smooth-edged.......... 3

3.(2b)

a. First dorsal fin larger than second and with angular apex; tip of pectoral angular.......... *Heteroscymnus**

b. First dorsal fin no larger than second and with rounded apex; tip of pectoral rounded.......... *Somniosus*

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* *Heteroscymnus* may differ from *Somniosus* in other characters, such as dentition or denticle structure, that were not fully described by Tanaka. If it does not, *Heteroscymnus* may be reduced to subgeneric rank or perhaps to the synonymy of *Somniosus*.

4.(1b)

a. Lower teeth erect. First dorsal fin more displaced backward, the end of its base over front part of pelvic base. Dorsal fins subequal. Subterminal notch in caudal fin definitely evident, though small. (Denticles quadrate, with median pit, but without root-like processes. Fins not clear-edged.).. *Isistius*

b. Lower teeth strongly bent outward. End of base of first dorsal fin well in advance of pelvic insertion. Second dorsal longer-based than first. Subterminal notch of caudal obsolescent.. 5

5.(4b)

a. Denticles triangular, keeled, ending in a spiny point. Base of second dorsal not more than one-half longer than base of first dorsal. Caudal axis moderately upturned; epaxial part of caudal distinctly less expansive than hypaxial part. Snout depressed. Fins entirely blackish, not clear-edged. (First dorsal without spine, beginning far in advance of middle of total length, over pectoral base. Snout much produced.)............*Heteroscymnoides*

b. Denticles quadrate, with central pit and with roots at the four corners. Base of second dorsal much more than twice as long as base of first dorsal. Caudal axis scarcely upturned; epaxial part of caudal about as greatly expanded as hypaxial part. Snout scarcely depressed. Fins blackish at base, transparent outward.. 6

6.(5b)

a. First dorsal with a definite spine, beginning before middle of total length, much nearer pectoral than pelvic base. Snout much produced and sharper...*Squaliolus*

b. First dorsal without trace of spine, beginning behind middle of total length, much nearer pelvic base than pectoral base. Snout blunt and broadly rounded. (Other differences outlined on p. 161.)..........*Euprotomicrus*

Description of Specimen

The body is essentially cylindrical in cross-section. In the region of the gill slits and in the anterior part of the trunk, where the area of cross-section is greatest, the width of the body equals its depth. The snout at its base is about 0.1 wider than deep. Toward the base of the pelvic fins the ventral surface becomes flattened and the width becomes restricted to about 0.7 the depth. Behind the end of the second dorsal base the body becomes depressed. Behind the pelvic fins a rectangular cross-section is gradually assumed, owing to the flattened lower and upper surfaces and the development of a ridge along the posterior part of the lateral line and of another ridge along the ventrolateral edge of the caudal peduncle. As the upper of these two ridges begins more anteriorly, the cross-section in the region below the second dorsal base, and to a slight degree farther forward, is somewhat pentagonal. Between the dorsals and in front of the first dorsal is a weak ridge along the midline. Between the anus and the base of the lower caudal lobe is a pair of moderately conspicuous grooves, rather close together. There are no precaudal pits. The distance from the tip of the caudal fin to the front of the anus is contained about 1.85 times in the distance thence forward to the tip of the snout. The greatest depth is contained 7.4 times in the length to the subcaudal origin. The least depth of the caudal peduncle is contained 1.6 times in the orbit (excluding the notches).

The ventral contour is nearly straight from the mouth to the caudal base. The dorsal contour curves gradually downward from above the end of the pectoral fin to the base of the caudal. As seen from the side, the head is almost bullet-shaped, with the snout very broadly rounded. As seen from above or below, the lateral contours converge forward in nearly straight lines to the rear of the nostrils, where the width is approximately equal to the preocular length. The outlines are strongly concave between the nostrils and the almost hemispherical tip of the snout. The snout is relatively short in front of the eye but moderately long in front of the mouth: the preocular length is contained 1.7 times in the preoral length, which approximates the distance from the middle of the mouth to the first gill slit.

The nostrils are unusually far forward and are more nearly lateral than ventral.. As seen from the front, their axes converge strongly downward, so that, if extended to a common meeting, they would approximate an equilateral triangle. The least distance between the nostrils, at the ventral end, is approximately 0.4 the greatest distance between the outer edges of the narial pores. These pores, which form the upper end of the nostrils and are directed almost straight forward, are oval in cross-section, with a vertical height about two-thirds the transverse diameter, which is about two-thirds the length of the pupil. Just below the pore, the posterior rim of the nostril is inturned as a blunt flap, which is overlain by the almost hook-like process at the upper end of the thin narial valve. The total height of the nostril approximates 0.5 the preocular length of the snout, and is about 0.5 greater than the least internarial distance. As seen from below, the nostrils form an angle of 130°. As seen from the front, they form an angle of 95°.

The subcircular eye cannot be covered by eyelids. The pupil is round. The horizontal diameter of the cornea is about 0.1 greater than the vertical. The upper orbital margin is formed by two lines diverging at 140°, each ending in a notch, of which the one in front is smaller and shallower than the one just behind the upper third of the eyeball. The lower margin of the orbit is approximately semicircular. The surfaces of the eyes converge downward at an angle of about 38°. The eye is bisected by the body axis. The interorbital is strongly convex.

The spiracles are very large. The width (height) is about equal to the length of the pupil, is about 0.5 the orbital diameter, excluding the notches, is about two-thirds the least distance between orbit and spiracle, and is about 0.25 the interspiracular distance. Their axes converge upward at an angle of 72°. They are located about midway, vertically, between the eye and the dorsal profile. Each spiracle is roughly semicircular, with the posterior edge nearly straight. Toward the front is a conspicuous crescentic septum, fimbriate on its posterior edge.

The gill slits are excessively short. The second and longest is approximately 0.5 as high as the spiracle. Posteriorly the height decreases to the fifth, which lies just in advance of the insertion of the pectoral fin. This last slit is hardly more than a pore, less than 0.25 the height of the spiracle.

The main part of the mouth is an almost transverse slit, with the perpendicular only about 0.1 the chord, which about equals the preocular length. From each angle there extends backward and slightly outward a deep groove, which is contained about 1.4 times in the width of the mouth proper. Around the corner of the mouth is a thick fold, completely hidden when the mouth is closed. The mandibular part of this fold is very short and weakly developed, whereas the anterior part is a very conspicuous soft fleshy structure lying in a deep recess, which is continued backward as the posterior groove and forward as a cavern. Within the corners of the mouth the suborbital skin forms a broad semicircle before it becomes attached toward the midline. From this region of attachment a fold of skin separates the upper jaw from the thick fold previously described. There is a corresponding but much thinner fold against the lower jaw. The pocket immediately in front of the upper jaw is deeper than the corresponding mandibular pocket, and has a fringed edge. The posterior grooves of the mouth converge to an angle of about 40°.

The teeth are extremely unlike in the two jaws. Those in service in the upper jaw form about 4 rows, with the teeth of the adjacent rows alternating, so that the tooth arrangement is in quincunx. Each tooth is narrowly triangular and needle-pointed and has a narrowly forked root. In the lower jaw, in contrast, only a single series functions. The lower teeth are bent outward, so that those near the center of the jaw diverge at an angle of about 43°. The outer exposed edge is weakly convex and only slightly oblique. The inner edge is strongly oblique and is slightly concave, especially toward the sharp tip. These lower teeth are very much compressed and have a flat outer surface, contrasting with the rounded outer surface of the much narrower upper teeth. The inner edge of each crown contacts the base of the crown of the next tooth inward and is overlapped by the strong, rather pointed shoulder of that tooth. The lower teeth number 11+1+10 (the 11 on the left side include a very small one in the rear). There is no trace of denticulations on either upper or lower teeth.

The denticles are of two types, both of which are quadrate, with incurved edges, laterally projecting roots from the corners, and a deep hollow center. They agree in showing no obvious distinction between pedicel and blade.

In about every fourth to sixth row of small denticles is one about 2 or 3 times as long on each side. These larger denticles have strongly concave margins and, in addition to the central pit, a pit in each angle. Some have additional pits around the periphery of the median one. To the naked eye, the smaller denticles are scarcely visible, but the large ones look like minute scattered warts. The pattern of the denticles is approximately uniform over the body and head.

The lateral-line pores are rather irregularly spaced. There are 60 between the verticals from the pectoral insertion and the origin of the upper caudal lobe. The series continues for about 8 pores along the anterior half of the caudal axis. The lateral line is continued forward as a series of 19 pores to one that lies just above the spiracle. The pore just anterior and inside the last-named pore is the outermost in a cross-commissure of 9. Near the midline, just in advance of this commissure, is a pair of well-separated pores. Anterior to the outermost pore of the commissure a slightly sigmoid row of 22 pores extends to opposite the front of the eye. The same series is continued forward, curving inward, toward the tip of the snout. On the interorbital region, inside the supraorbital row on each side, is a considerable scattering of pores. Pores are also scattered behind the upper posterior part of the infraorbital series, and across the lower part of the snout, between the middle sections of these series. The preorbital file, however, is simple. On the lower side of the snout the pores tend to be concentrated in a zigzag cross-commissure and in a rather V-shaped file behind the inner tips of the nostrils.

There are no obvious luminous organs. In life, however, the skin was very slimy and it is not impossible that the mucus may be luminous.

There is no trace of spines in any of the fins, either in external view or on the X-ray plates. The dorsal fins are very dissimilar in size. The base of the anterior fin is hardly as long as the eye. It begins midway between the margin of the caudal fin and the middle of the eye (it is indicated in the figure about one pupil-length too far forward). The upper-anterior angle of this fin is very broadly rounded and the upper-posterior angle is sharply pointed. The height of the fin is about twice its basal length. The interdorsal space is 0.3 longer than the distance between the end of the second dorsal base and the beginning of the upper caudal lobe. The base of the second dorsal is about thrice as long as that of the first, and in depressed length more than twice as long. Its upper-anterior angle is very broadly rounded and its posterior tip is sharply pointed. The vertical from the origin of the first dorsal is 3.5 times as far from the end of the pectoral base as it is from the pelvic insertion. The origin of the second dorsal is approximately over the posterior end of the pelvic base. The distance from the tip of the second dorsal to the beginning of the upper caudal lobe is approximately equal to the length of the orbit, including the notches.

The caudal fin is nearly symmetrical, with both lobes greatly expanded. The fleshy axis expands before its middle to a width about 0.5 greater than the least depth of the peduncle. The posterior, acuminate tip of the urostyle reaches the margin on the lower posterior edge of the upper lobe. There is, however, little trace of a subterminal notch. The vertical expansion of the upper lobe approximately equals that of the lower, but since the upper lobe begins a pupil's length farther back and has a more oblique front edge, about half its area is behind the tip of the lower lobe. The angle formed by the slightly convex front edges of the lobes is 79°. Each lobe is broadly rounded, with a weakly convex posterior edge. The margin of the lower lobe slopes upward and slightly backward; that of the upper lobe, upward and slightly forward. The upper-posterior margin of the lower lobe, below the end of the urostyle, is rather evenly and deeply concave. The distance between the tips of the lobes is nearly 0.2 greater than the distance between the origin of the lower lobe and the tip of the urostyle.

The pectoral fin in ventral view forms roughly an equilateral triangle, with the anterior and posterior edges moderately convex and the lower-posterior angle broadly rounded. The upper or anterior half of the fin is approximately horizontal; the lower, or posterior, part, arched downward. The fleshy pelvic bases are approximately flat and horizontal. The pelvics are elongate basally, very broadly rounded at the outer-anterior corner, and very sharply pointed on the inner-posterior angle. The outer edge is concave just in advance of the sharp posterior tip. The fins are in contact over and behind the anus, in a straight line about two-thirds the greatest length of the fins. The tips extend to behind the vertical from the middle of the second dorsal base. Just behind the anus, between the inner ends of the pelvic bases, is a pair of valve-like flaps.

Perhaps in correlation with the dwarf size, the segments are very few. Between the front edges of the paired fins about 22 muscle bands are indicated by slightly depressed and slightly darkened lines crossing the belly. The myomeres are very weakly angulated on the sides and on the belly. The individual vertebrae, clearly evident in the X-ray photograph (plate VI), are elongate and much constricted medially so that the adjoining halves form spindles, much as in a teleost. There are only 48 between the head and the origin of the upper caudal lobe. Along the axis of the caudal fin the vertebrae become much reduced and difficult to see in the X-ray photograph. There are 6 vertebrae anterior to the insertion of the pectoral fin, 21 between the insertions of the paired fins, and 21 between the pelvic insertion and the origin of the upper caudal lobe. The contrast between these vertebrae and the disc-like vertebrae of most sharks is very great, but the condition in *Euprotomicrus* is approached by that in certain other squaloid sharks (Hasse, 1879–1885).

The fins are only partly covered with denticles. The pectoral has a thick covering on its basal third to two-fifths, with a further extension outward near the front edge. The pelvic has denticles only on the swollen fleshy base. The caudal is well covered over the fleshy axis and outward over two-thirds to one-half of each lobe. The dorsals are almost entirely devoid of denticles, except at the extreme base. Beyond the area covered by denticles, the fins are extremely thin and flexible and clearly show the ceratotrichia.

In the water this little shark appeared brown, but when brought on deck seemed blackish. Some myctophids exhibit a similar apparent color change. In alcohol the specimen is blackish, with purple and brown sheens. The blackish body color extends over the denticle-covered part of the fins, with diffusion somewhat farther out. The outer edges of the fins, however, are crystal clear, in a pattern well shown in the figures. The urostyle is black to its slender tip. The concealed parts of the mouth are whitish, as is also its anterior exposed margin medially. The thin outer part of the narial valve is clear of pigment.

When seen at the surface the little shark was swimming slowly with an undulatory movement, progressing in an approximately constant direction as though it was not especially attracted by the light. A first miss with the dip-net did not seem to frighten it. It showed extremely little activity when picked out of the net and even when placed in formalin did not become very active. It was very slippery, owing to a profuse coating of slime. Quantities of mucus were exuded onto the net.

Proportional Measurements

The measurements are expressed in thousandths of the total length (233 mm.). They were made before the specimen was transferred from formalin to alcohol. In comparison, proportions for a few critical measurements are given for the holotype, 192 mm. in total length, on the basis of measurements made for us through the kindness of Dr. Léon Bertin.

Body.—Predorsal length, from tip of snout to extreme front edge of dorsal base, 527 (521 in type). Distance between dorsal origins, 152 (167 in type). Interdorsal space, 122. Origin of second dorsal to margin of upper caudal lobe, 314. Tip of second dorsal to caudal margin, 190. Pectoral insertion to dorsal origin, 300 (312 in type). Prepectoral length, 245. Prepelvic length, 614. Between insertions of paired fins, 379. Greatest body depth, 116. Least depth of caudal peduncle, 21. Greatest body width, 117. Width of caudal peduncle at front of caudal fin, 22.

Head.—Length to nearest point of first gill slit, 189 (177 in type). Width between first gill slits, 111. Preocular length of snout, 63. Preoral length of snout, 102. Snout tip to outer end of nostril, 34. Nostril length, including dorsal pore, 30. Least internarial width, 21. Width between inner edges of dorsal pores of nostrils, 40. Width between tips of narial flaps, 53. Least distance from nostril to orbit, 33. From nostril to mouth, 72. Front of mouth to line joining ends of gape, 52. Width between outer edges of concealed lips, 67. Width between ends of oral grooves, 92. Orbit to end of oral groove, 60. Orbital notch to end of oral groove, 63. Least suborbital width, 24. Orbit length, between inner edges below notches, 36. Between extreme ends of orbital notches, 46. Orbit height, 30. Fleshy interorbital width, 82. Width between orbits, ventrally, 68. Least interspiracular distance, 69. Postorbital notch to spiracle, 30. Between outer-ventral and inner-dorsal ends of spiracle, 20. Anteroposterior width of spiracle, 13. Spiracle to end of oral groove, 38. Spiracle to pectoral insertion, 110. Between front of first and fifth gill slits, 50. Longest gill slit, 16.

Fins.—First dorsal: base, between extreme ends, 29; origin to upper-anterior tip, 46; upper-posterior edge, 31; lower-posterior edge, 37. Second dorsal: base, 86 (88 in type); origin to upper-anterior tip, 39; upper edge, 104; lower-posterior edge, 50. Caudal: upper lobe, extreme origin to farthest point, 142; lower lobe, origin to tip, 120; dorsal origin to tip of urostyle, 129; dorsal origin to nearest point on margin, 102. Pectoral (appressed against body): base, 39; insertion to upper-posterior tip, 98 (89 in type); to lower-posterior tip, 101; posterior edge, 85; extreme width, 91; lower posterior edge, 71. Pelvic: base, 68; insertion to outer-anterior tip, 55; outer-posterior edge, 72; inner-posterior edge, 48.

Summary

A very peculiar small shark collected at the surface over deep water nearly 500 miles off California is identified as *Euprotomicrus bispinatus* (Quoy and Gaimard). It is the second specimen of the genus known from the Pacific Ocean. *Euprotomicrus* is regarded as monotypic, since *Squaliolus,* also treated as monotypic, is interpreted as generically distinct. *Euprotomicrus hyalinus* Eigenmann and *Squaliolus sarmenti* de Noronha are synonymized with *E. bispinatus* and *S. laticaudus* Smith and Radcliffe, respectively. *Euprotomicrus* is a highly modified squaloid shark referable to the Dalatiidae as currently defined. Generic relationships within this group are rendered uncertain because of convergent evolution. Many species show primitive and specialized features in confusing combinations. The validity of the separation of the Dalatiidae from the Squalidae is discounted, for the dorsal spines seem to have become lost on several phyletic lines. Echinorhinidae is also synonymized with Squalidae. Provisionally these groups are retained as subfamilies, Dalatiinae and Echinorhininae. The dalatiine genera seem to form two main lines (see analytical key, p. 164). The new specimen is described and its measurements are listed.

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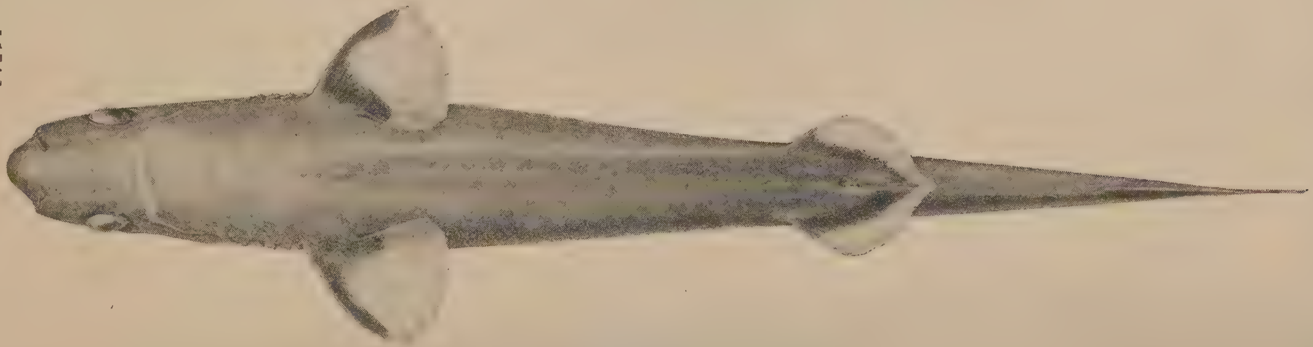

PLATE IV

FIGURE 1. Lateral view of a 233–mm. female specimen of *Euprotomicrus bispinatus*, a peculiar little shark captured at the surface nearly 500 miles off California. All drawings by Alma Froderstrom.

FIGURE 2. Ventral view of the same specimen.

PLATE V

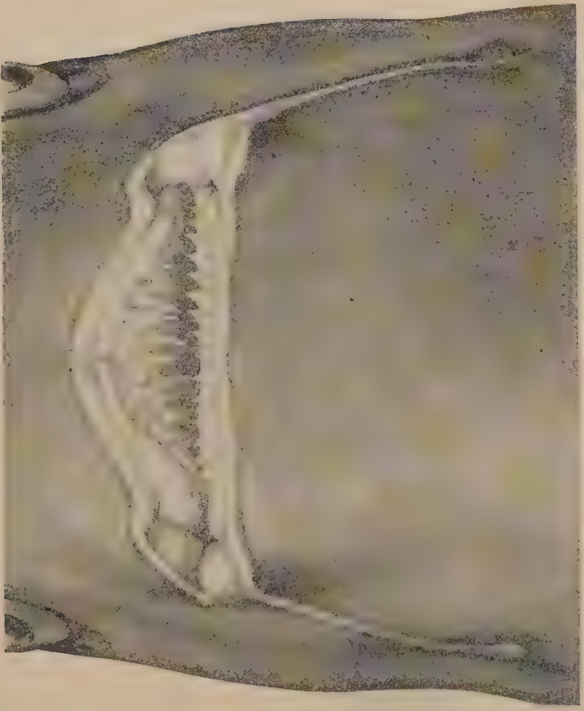

FIGURE 1. Mouth and teeth of the same specimen.

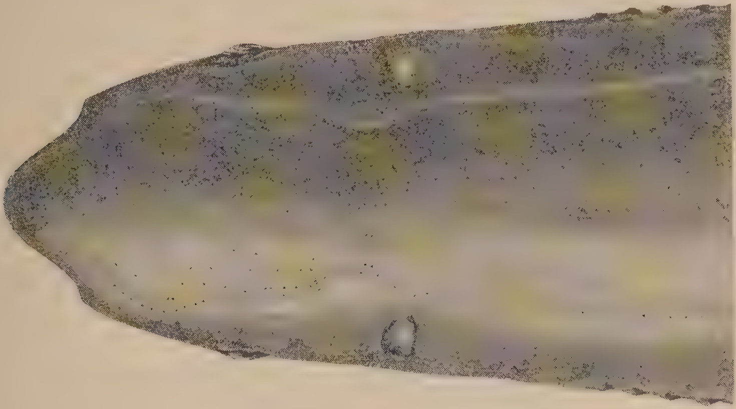

FIGURE 2. Top of head of the same specimen.

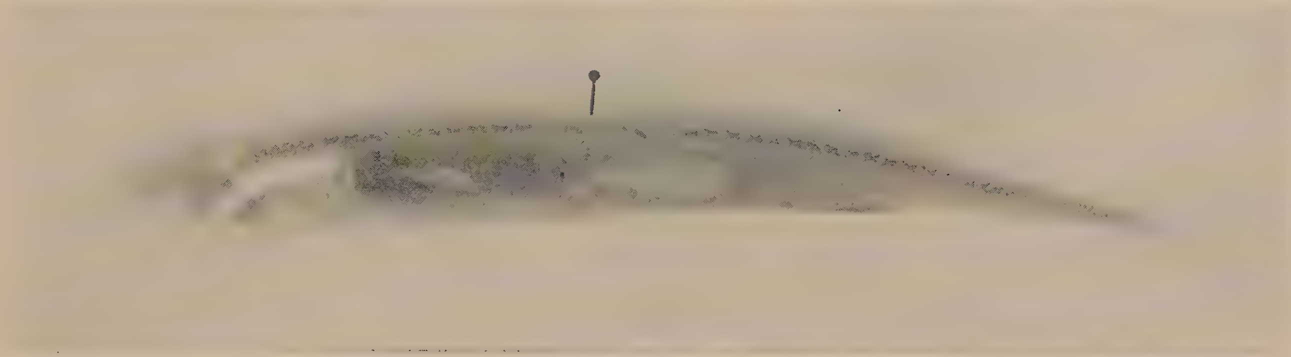

PLATE VI

X-ray photograph of the same specimen, to show, in particular, the vertebrae, which are elongate and much constricted medially, so that the adjoining halves form spindles. Photo by J. L. McHugh.

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Reprinted from Journal of Mammalogy
Vol. 32, No. 3, August, 1951, pp. 365–366
Printed in U.S.A.

PROBABLE RECORD OF THE BEAKED WHALE, *ZIPHIUS CAVIROSTRIS*, IN BAJA CALIFORNIA

In this journal (Vol. 27: 241–44, 1946) I reported a specimen of *Ziphius cavirostris* Cuvier that was stranded at Del Mar, Southern California, as the first record for the Pacific Coast south of British Columbia. Since then Orr (Jour. Mamm., 29: 420–21, 1948) has listed another, from northern California. Since the species (or species group) is cosmopolitan, further records, still farther south, have been anticipated. The highly probable occurrence of this beaked whale in Baja California may now be reported.

Early in December, 1950, a cetacean that appears almost certainly to have been of this species was found by Mr. H. L. Goddard, of Carlsbad, California, stranded on the beach of San Ramón, at the south end of the lagoon at the mouth of Río Santo Domingo, at 30° 42.7′ N. Lat. According to Mr. Goddard it was 18 feet long and had typical whale flukes.

He says that the lower jaw projected about 4 inches and caried at its extreme tip a pair of strong erect teeth implanted in the flesh less than an inch apart. The tooth that he removed is 59.0 mm. long, 21.5 mm. in lesser diameter, and 30.5 mm. in greater diameter. The maximum width is well above the base, but considerably below the middle of the height of the tooth. The correspondence is very close with a tooth of this species figured by True (U. S. Nat. Mus., Bull. 73: pl. 38, figs. 10–11, 1910). The number, size, position, and erect orientation of the teeth appear to be diagnostic of *Ziphius*. The only possible confusion would seem to be with *Hyperoodon*, which has not yet been reported reliably from the northeastern Pacific.

The tooth is deposited in the mammal collection of the San Diego Society of Natural History (No. 2631).—CARL L. HUBBS, *Scripps Institution of Oceanography (University of California), La Jolla, California. Received January 8, 1951.*

[Contributions from the Scripps Institution of Oceanography, New Series, No. 523.]

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Reprinted from SCIENCE, July 6, 1951, Vol. 114, No. 2949, pages 7–9.

ubmarine Canyons: A Joint Product of ivers and Submarine Processes[1]

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The abandoned sea-level-lowering hypothesis. This ote is written in the hope that the writer will not ontinue indefinitely to be tied to the now long-disarded hypothesis that submarine canyons are the reult of a lowering of sea level amounting to several housand feet, which was thought to result from the ormation of huge ice caps. This hypothesis was ffered as a somewhat forlorn hope that seemed, at he time, to be the only way out of an enigma. Disoveries of the past few years have indicated that no uch great lowering took place during the Pleistocene. he large submergences indicated by a considerable eries of oceanographic discoveries appear to be more emote in age and to have, therefore, no relation to lacial control. Despite recent articles (*1*) and talks iven before scientific societies during the past two ears it has proved most difficult to bury the old ypothesis. In offering an alternative explanation with ttle amplification it should be noted that a much onger article is being prepared. This will give a comlete account of the basis for suggesting still another rigin for the much-abused submarine canyons.

A new composite hypothesis. New oceanographic nformation can now be combined with information rom drill cores along the coasts and on islands to uild a composite hypothesis that accounts for subarine canyons without appealing either to enormous ovements of land or of sea level or to the excavation y powerful submarine currents for which there is no vidence. It now appears that many of the canyons ave three divisions as follows:

1. Inner valley heads that extend into shallow water long many coasts and contain indications of having been ut at a relatively recent period.
2. Intermediate canyons that have rocky walls rising undreds or even thousands of feet above their narrow. inding floors.
3. Outer valleys, only slightly incised into great masses f unconsolidated sediment, which can be traced out to he base of the oceanic slopes.

These three divisions are not clearly separated one rom the other and apparently have had a composite nd overlapping origin. The outer two divisions can e explained by a sequence of events that fits into a attern well known to geologists who have investiated the history of depositional basins (geosynlines). The submergence of a geosyncline is known o alternate with reversals of movement. Similarly, the leep submergence of the continental margins, which s thoroughly established from well records along many of the present coasts, was probably interspersed with stages of uplift or preceded by an uplift. During uplifts, the exposed continental margin was trenched by stream erosion, thus forming the intermediate canyons. Outside these canyons deltas developed on the lower oceanic slopes.

Following the cutting of the canyons, the slopes were submerged. The canyons became a locus of intensive deposition, but wherever they had high gradients the sediment was carried outward by submarine landslides such as are now well established as occurring in the canyons along the California coast. The soft sediments of the deltas are thought also to have undergone mass sliding movements, opening up cracks and scars on the delta fronts. One of the results of the slides was the development of turbidity (density) currents which transported the sediments down the canyon floors (*2*) and, moving across the deformed deltas, sank into the landslide scars and cracks, gradually transforming them into valleylike features. These "valleys" were eventually extended to the base of the continental slopes.

As submergence continued, deposits were formed in many places on the old surfaces into which the canyons had been cut. These deposits built up shelves such as those on the east coast of the U. S., but failed to eliminate the canyons because of the continuing landslides. Slides probably also took place on the continental slopes. In this way the canyons have walls that have grown upward as a result of deposition as the canyon floor sank.

During the glacial period, which lasted approximately one million years, the canyon heads were alternately exposed and submerged as the result of changing sea levels. During each glacial stage of lowered sea level the streams from the land have tended to flow into the heads of the canyons and have extended these heads farther in toward the present coasts. It is probably this stream erosion during glacial stages that accounts for the fresh appearance of canyon heads in shallow water (*3*).

The history of canyon development has been different in different areas. For example, in some regions, such as in Monterey Bay, California, the middle zone of the canyons extends far deeper than in most other areas, and the movements of both uplift and sinking appear to have been much greater. The upbuilding of the shelf during submergence has been very great along the northeast and Gulf coasts of the United States, but south of Cape Hatteras the shelf has apparently not been covered with sediment as it sank, with the result that the deep Blake Plateau represents a submerged shelf swept clean by bottom currents.

Evidence for the new hypothesis. The sequence of events described here is not a purely philosophical concept built up to explain a very puzzling situation, as some of the preceding hypotheses have been; it is built on a substantial and rapidly growing foundation of facts from marine investigations and from drill core loggings. A brief summary of the evidence, which will appear in full later, follows.

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[1] Contribution from the Scripps Institution of Oceanography, New Series No. 524.

1. The inner canyons, where studied in detail (off La Jolla, off Carmel, and off the French Riviera), have an extraordinary resemblance to adjacent stream-cut canyons; that is, they have winding courses, branching tributaries, rock gorges with precipitous walls, and even terraces on the side.

2. There are many lines of evidence to support the contention of great submergence along the continental borders and in oceanic island masses. Deep wells along some of the coasts of the continents show that shallow water, or even terrestrial deposits, extend for thousands of feet below present sea level. Wells that significantly bear out these contentions have been drilled on Cape Hatteras and the Mississippi delta, the two points in the U. S. where deposition has extended the land out across the greater part of the continental shelf. Numerous other wells along the east and south coasts of the U. S. add confirmation, as do some well records of coastal California. Similar results come from wells drilled into oceanic islands, like Bikini (*4*). Rounded cobbles, indicative of wave action in shallow water, are found widespread on the banks and seamounts outside the continental slopes. Fossil evidence reported by R. S. Dietz, Maurice Ewing, and most recently by Roger Revelle indicates that these banks were covered only with shallow water at a time that probably preceded the ice age by many millions o years.

3. Channels similar to those found on steep delt fronts are found outside the rock canyons along th southern California coast, and these channels exten down the sides of bulging masses indicative of ancien deformed deltas.

4. There is no present evidence that either slumpin or mud-laden currents are capable of excavating grea rock-walled canyons like those on the sea floor. I fact, the steep fronts of deltas built into lakes in th Alps are known to be building out rather than havin canyons cut into them.

5. The slight depressions in the fronts of lake delta probably represent localities where currents or slide have locally slowed the forward advance of the delt These channels have little in common with the roc gorge type of submarine canyons but resemble th outer shallow valleys that form an extension of th submarine canyons.

6. Virtually all the arguments now being used fo subaerial origin are based on the hypothesis of grea lowering of sea level during the ice ages, an idea tha was abandoned more than two years ago.

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(Reprinted from: Stanford Ichthyological Bulletin, Vol.4, no.1, pp. 7-10.
Dec. 27, 1951.)

DYSOMMINA RUGOSA, AN APODAL FISH FROM THE NORTH ATLANTIC, REPRESENTING A DISTINCT FAMILY[1]

By James Böhlke and Carl L. Hubbs
Stanford University and Scripps Institution of Oceanography

The strange eel here considered was first described in manuscript by Hubbs in 1916, as part of a collaborative report with the late Dr. C. H. Gilbert. A recent re-examination of a specimen by Böhlke[2] brought the problem up again, resulting in a combination of the two independently written manuscripts. Just as our paper was going to press, with the species named for Dr. Jordan, a description of what appears to be the same form has been published by Ginsburg (1951). As our conclusions differ notably from his, our paper is allowed to stand almost unchanged except for the use of Ginsburg's names.

DYSOMMINA Ginsburg

Dysommina Ginsburg, 1951, p. 450 (type *D. rugosa* Ginsburg).

Body elongate, compressed, slender. Anus far in advance of mid-length. Scales absent, skin smooth. Lateral line indistinct, evidently beginning rather high on body anteriorly, descending to middle of tail. Eyes covered by a layer of skin, placed anterior to mouth angle. Snout long, rounded, projecting beyond the lower jaw, and covered, as the lips and lower jaw, by small papillae. Mouth cleft wide, horizontal, lateral. Anterior nostril tubular, near tip of snout; posterior nostril with flared rim, enlarged to form a flap anteriorly, lateral, immediately in advance of eye. Teeth small, sharp, in bands on maxillaries and mandibles; four or five large, conical, widely spaced teeth set in pockets on the shaft of the vomer. Branchial apertures crescentic, oblique to nearly horizontal, below pectoral base, well separated below. Dorsal commencing behind head, anal before mid-length of body and immediately behind anus. Caudal well developed, pointed, confluent with dorsal and anal fins. Membranes of vertical fins thick. About 16 branchiostegals.

Frontals and parietals paired. Mesethmoid a thin V-shaped element, shaped like a tear-drop in cross-section, fused with vomer. Pterygoid bones everywhere reduced to thin splints. Prootic thin, little flattened anteriorly, expanding into a bulb posterodorsally. Maxillaries and mandibles long and thin, bearing wide bands of teeth. Hyomandibular one of the largest bones, composed of a strong ridge and supporting shelves that are equal in width to the wide head of the bone. Opercle elongate and low, originating on lower one-half of hyomandibular. Basioccipital-vomerine axis virtually straight. About 13-16 rudimentary gill rakers on lower limb of first arch. Slit behind fourth gill reduced to about one-half length of lower first gill arch.

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[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 525.

[2] The kindness of Doctors Alexander Wetmore and Leonard P. Schultz of the National Museum has now permitted the permanent retention of one example at Stanford.

Dysommina rugosa Ginsburg

Dysommina rugosa Ginsburg, 1951, p. 450 (Albatross Station 2667, off Cumberland Id., Georgia).

Two examples: USNM 44324, collected with large beam trawl by the U.S. Fish Commission Steamer "Albatross" in the Gulf Stream off southern Georgia, at Station 2669, 31°09'00" North Latitude, 79°33'30" West Longitude; May 5, 1886; depth 352 fathoms; bottom temperature 43.7°F.; bottom recorded as gray sand and dead coral. SU 24284, 215 mm. in total length, collected with the previous example.

Description: Measurements of no. 44324 in mm.: total length 289, head length to anterior end of gill opening 41.5 (.14 of standard length), tip of snout to dorsal origin 56 (.19 of standard length), tip of snout to anal origin 89 (.31 of standard length), greatest body depth 21, length of snout 15, eye diameter 4, fleshy interorbital width 7, gape 22, pectoral fin length 7, longest caudal fin rays 8.

Head and trunk contained just over three times in total length. Greatest depth of body 2.0 (1.9)[3] in length of head, 13.8 (14.3) in total length. Head 7.0 (7.4) in total length. Eye diameter contained 10.4 (9.7) in head length, 1.8 (No 24284 damaged) in interorbital width. Snout length 2.8 (2.9) in length of head, 19.3 (21.5) in total length. Gape extending slightly less than an eye diameter beyond eye, its length 1.9 (2.0) in head length.

Maxillary teeth in 4 or 5 wavy, irregular rows; those on mandibles similar, in bands which are widest anteriorly. Vomerine teeth consist of 4 or 5 much enlarged canines (posterior one lost from no. 24284), widely separated, set in individual pockets on the shaft of the vomer, their bases enclosed in the folds of skin which line the roof of the mouth much as in some of the dysommids. In fact, with the exception of the pair of anterior vomerine teeth which are present in *Dysomma anguillare* Barnard and absent in this new species, the entire dentition in the upper jaws of these fishes is strikingly similar. Tongue adnate. Postorbital region of head supported by the branchiostegals, some of which are visible through the skin of the branchial region.

Dorsal fin commencing posterior to tips of appressed pectorals, continuous, the distance from the tip of the snout to its origin contained 5.2 (5.2) in the total length. Distance from tip of snout to anal origin 3.2 (3.2) in total length. Vertical fins confluent around end of tail, the tip pointed; longest caudal rays 5.2 (4.3) in length of head. Small pectorals covered by rather heavy skin, their length 5.8 (5.3) in head length, 41.3 (39.1) in total length.

Pores not obvious in the lateral line proper. The only conspicuous pores in the lateral line system of the head are the elongate, open pores of the mandibular series, 4 very obvious pores in the infraorbital series (posterior to the anterior nostrils), and a single pore just posterior and median to either anterior nostril.

Color in alcohol uniformly light tan, with small groups of melanophores more or less evenly spaced along mid-line of body. Peritoneum black.

Relationships: Ginsburg's genus cannot properly be placed in any of the described eel families as currently defined (Regan 1912, p. 379; Trewavas 1932, p. 656). In external appearance and tooth pattern this genus bears a strong resemblance to several of the dysommids, but its enlarged otic bulla and paired frontals in particular are characters which would place it near the Heterenchelidae, Moringuidae, and the genus *Kaupichthys* (see Gosline 1950, p. 313). It resembles the Moringuidae in having the palatopterygoid reduced to a splint and the vomer ankylosed with the ethmoid; it differs

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[3] Proportions for no. 24284 in parentheses.

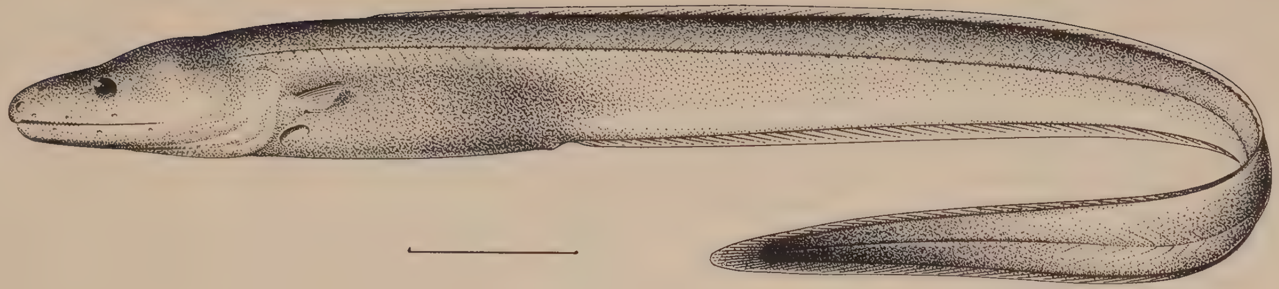

FIG. 1. *Dysommina rugosa* Ginsburg. USNM no. 44324. (Drawn by the late William Sackston Atkinson. Reproduced from a photo of the original drawing in the files of the Division of Fishes, U. S. National Museum.) Line represents one inch.

from that family, however, in having the tail much longer than the trunk, vertical fins that are not confined to the tail, and bands of teeth on the maxillaries and mandibles (versus uniserial on mandibles and uniserial or absent on maxillaries). Ginsburg's genus resembles the Heterenchelidae in having the tail much longer than the trunk, but differs trenchantly from that family in having the vomer ankylosed with the ethmoid rather than being separated by a suture, and the palatopterygoid reduced to a splint rather than being well developed and laminar. The new genus resembles *Kaupichthys* in having the trunk shorter than the tail and in lacking a suture between ethmoid and vomer. It differs from that genus, however, in having the posterior nostrils lateral rather than labial and tubular, in having the palatopterygoid reduced to a thin splint rather than well developed and laminar, and in the different character and shape of the branchial openings.

On the basis of the characters indicated above and by reason of its very distinctive external appearance, *Dysommina* should stand, at least provisionally, as the type of a distinct family of apodal fishes, the Dysomminidae.

Thanks for assistance in the study of this new eel go to the late Dr. Charles Henry Gilbert, who long ago placed the old "Albatross" collections in Hubbs' hands for a collaborative report that remains in manuscript; to Dr. Leonard P. Schultz of the National Museum, for the loan of the specimen and the accompanying illustration; to Mr. Norman J. Wilimovsky of Stanford University, for assistance in the osteological preparation; and to Dr. George S. Myers of Stanford, for advice throughout.

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Reprinted from Copeia, 1951, No. 4

IDENTIFICATION AS OSMERIDS OF TWO FISHES DESCRIBED FROM THE NORTH PACIFIC AS PARALEPIDIDS.[1]—For some time we have both suspected that *Sudis squamosa* Chapman (1939, Proc. U. S. Nat. Mus., 86: 519–22, fig. 63) and *Lestidium* (*Bathysudis*) *parri* Chapman (*ibid.*: 522–24, fig. 64), both described from specimens caught in plankton hauls off Alaska, might not belong to the "Sudidae" (Paralepididae); and now Robert R. Harry, in his revision of the Paralepididae, has come definitely to the conclusion that neither nominal species should be included in the family to which it was assigned. To clarify the identification of these two species we examine the holotypes at the U. S. National Museum.

The holotype and only known specimen of *Sudis squamosa* (USNM No. 108150), from off the southern shore of the Alaskan Peninsula, proves without question to be a half-grown Pacific capelin, *Mallotus catervarius* (Steller, in Pennant, 1784, Arctic Zoology, 1: cxxvii). Comparison of specimens discloses no differences. Obviously, at least some capelin retain a pelagic habitat until they are half-grown. As Schultz (1937, Proc. U. S. Nat. Mus., 85: 13–20) has shown, *catervarius* is the oldest name for the Pacific form of *Mallotus*. We do not concur in a recent rejection of this name in favor of *M. villosus socialis* (Pallas), on the basis of the statement that Pennant, 1784, was "non binominal" (Berg, 1948, Ribi Presnich Bod SSSR i Sopredelnich Stran ["Fresh-water fishes of the U. S. S. R. and neighboring countries"], Akad. Nauk, 4th ed., 1: 452). After examining the original treatise we believe that the name *catervarius* can be retained, even though Pennant did not consistently employ binominal nomenclature. Steller, though pre-Linnaean, was binominal, and his names, including *"Salmo Catervarius* of Steller," would appear to have acquired availability when published by a post-Linnaean author, in this case Pennant. Pennant indicated that Pallas supplied the fish accounts from the manuscript of Steller. Pallas was also a binominal author.

The holotype of *Lestidium* (*Bathysudis*) *parri* (USNM No. 108140), from off Prince William Sound, Alaska, is just as surely identifiable as an eulachon, *Thaleichthys pacificus* (Richardson). It is a young specimen in the pelagic "Eperlanio" stage (Hubbs, 1925, Proc. Biol. Soc. Washington, 38: 53).

The agreement between these holotypes and comparable specimens of *Mallotus* and *Thaleichthys*, respectively, extends to details of dentition, to superficially apparent features of anatomy, and to other characters indicated in our respective treatments of the systematics and the osteology of the osmerids (Hubbs, *op. cit.*; Chapman, 1941, Jour Morph., 69: 279–301, figs. 1–15). The items of precise correspondence include details of pigmentation.—Carl L. Hubbs, *Scripps Institution of Oceanography* (*University of California*), *La Jolla, California,* and Wilbert M. Chapman, *American Tunaboat Association, San Diego, California.*

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[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 526.

THE LIFE CYCLE OF THE DICYEMID MESOZOA

BY

BAYARD H. McCONNAUGHEY

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY AND LOS ANGELES
1951

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOÖLOGY
EDITORS (BERKELEY): A. H. MILLER, R. M. EAKIN, HAROLD KIRBY, CURT STERN
Volume 55, No. 4, pp. 295–336, 13 figures in text

Submitted by editors February 26, 1951
Issued August 28, 1951
Price, 50 cents

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY AND LOS ANGELES
CALIFORNIA

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CAMBRIDGE UNIVERSITY PRESS
LONDON, ENGLAND

PRINTED IN THE UNITED STATES OF AMERICA

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THE LIFE CYCLE OF THE DICYEMID MESOZOA

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INTRODUCTION

The dicyemids are small vermiform organisms occurring in large numbers attached to the renal organs of various cephalopod mollusks. The simplicity of their morphology indicates that they belong very low in the phylogenetic scale of the metazoa, but in spite of extended studies of the group by several zoölogists little agreement has been reached about their classification or life cycle. Part of the life cycle still remains unknown.

Much of the conflict of views stems from the fact that generalizations have been made from observations on particular species or a few individuals without sufficient comparative basis. This has caused confusion in the study of other species in which the phenomena differ slightly. Another source of difficulty is that the most thorough studies seem to have been made on more specialized members of the group which are in some ways less favorable for study, particularly in phenomena relating to the accessory nuclei in the axial cell of the rhombogen phase. Secondary phenomena make this particularly difficult in some species.

Rather than present here the different schemes proposed by various authors, it has seemed expedient to take up the various phases of the life cycle in order, starting with the infection of young cephalopods, to discuss each in detail, and finally to summarize the life cycle as interpreted by the author, pointing out where this interpretation agrees with and where it differs from previous accounts.

The present paper is the second part of a study of the dicyemids; the first part, the taxonomic part, has already appeared (McConnaughey, 1949). The work was conducted at the Scripps Institution of Oceanography under the auspices of the Department of Zoölogy, University of California, Berkeley. The writer is greatly indebted to Dr. Harold Kirby and the late Dr. S. F. Light of the University of California; to Dr. Dennis L. Fox, Dr. Wesley R. Coe, Dr. Carl Hubbs, Dr. Henry Kritzler, and Mr. Sheldon C. Crane of the Scripps Institution of Oceanography; and to Dr. Horace Stunkard of New York University for aid and suggestions.

INFECTION OF YOUNG CEPHALOPODS

It is not known how the young cephalopod acquires its infection. I have examined over a hundred octopuses from the littoral zone along the coast of southern California and a few dredged specimens from slightly deeper water. All of them, with the exception of one very small dredged specimen, were already infected, though the smallest ones were much less richly populated by the parasites. A number of the individuals of this series were very small and immature, weighing less than a gram. Similar results have been obtained by other investigators along the Atlantic coast of Europe, the North Sea, and the Mediterranean. Pelagic species as a rule

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Contribution from the Scripps Institution of Oceanography (new series), number 527, and the Department of Zoölogy, University of California, Berkeley.

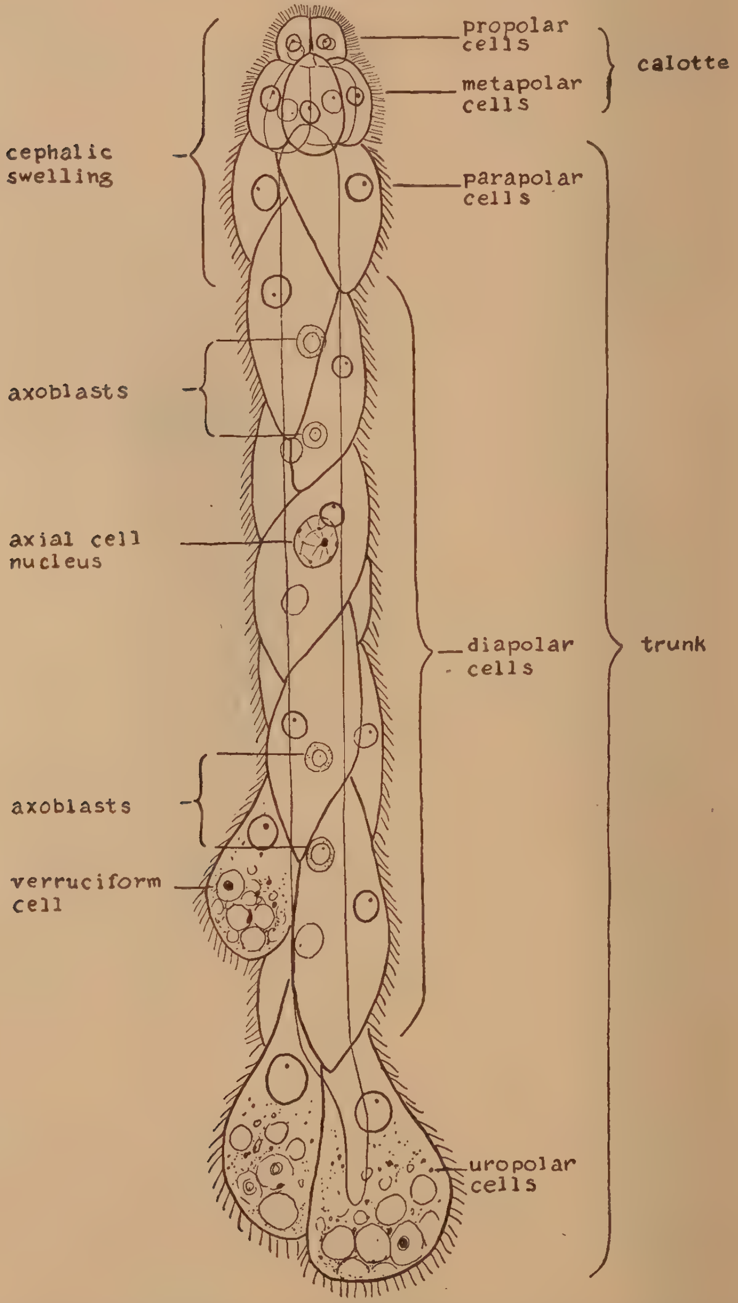
propolar cells
metapolar cells
calotte
cephalic swelling
parapolar cells
axoblasts
axial cell nucleus
diapolar cells
trunk
axoblasts
verruciform cell
uropolar cells

Fig. 1. Generalized drawing of a young dicyemid showing the terms that have been applied to various parts of the body. All figures in this paper, except where otherwise indicated, are camera lucida drawings from preparations in the author's collection.

are not infected. I have examined also sixteen octopuses from the reef around Oahu Island, T. H. and one from Kwajalein Island in the Marshalls. None of these was infected.

It is evident from these observations that the infecting agent is very abundant but apparently confined to relatively shallow waters. It seems not to have been introduced to certain oceanic islands separated by great distances of deep water from the nearest land. In favorable areas it appears to infect 100 per cent of the cephalopods present. Furthermore, the infection takes place very early in the life of the cephalopod, long before maturity.

If infection occurs through ingestion of an intermediate host, it would seem that this host must be very small, abundant, and itself so universally infected that none of the small cephalopods fail to acquire the parasites. The situation suggests that infection is accomplished directly from the female to her young or by some active free-swimming agent that seeks out and penetrates the cephalopod. Lameere (1916), Nouvel (1933), Gersch (1938), and I have all examined young octupuses freshly hatched from eggs in the laboratory and have found no evidence of infection in them. An opportunity for direct infection from the female to her young at the time of hatching is provided because the female deposits her eggs in recesses in the rocks and broods them until they are hatched. Meanwhile the mother is constantly liberating infusoriform larvae.

I have exposed freshly hatched octopuses and squids to large numbers of infusoriform larvae and watched them under a dissecting microscope. The infusoriforms were not attracted to the young cephalopods and no evidence of infection was found in exposed individuals with as much as a four-day exposure. Furthermore, the fact that adult male and female octopuses were both found to liberate infusoriforms at all times of the year in or out of the breeding season indicates that the infection probably does not proceed directly from one octopus to another.

The most probable method is active invasion by swarming larvae, presumably liberated from some other host. It is probable that the larval stem nematogens discovered by Lameere (1916) are the infective agents.

That additional infections often take place in the same octopus is indicated, as Whitman (1883) first clearly demonstrated, by the fact that it is not unusual to find two or even three species of dicyemids in the same individual cephalopod. When this occurs it is found that they are partly isolated from one another on different lobules of the kidney or at least in well-defined clusters, and that the predominant form is usually better developed and in a more advanced stage than the less predominant.

THE STEM NEMATOGEN

The earliest forms of dicyemid usually seen in young cephalopods are vermiform individuals, the so-called primary nematogens—nematogens that have developed directly as such from embryos without functioning as rhombogens at any previous time (fig. 1).

Lameere (1916) announced the discovery in very young *Sepia* and *Octopus* of a new phase of the life cycle of *Dicyema truncatum* and *Microcyema vespa,* preceding and giving rise to the primary nematogen. He named this the stem nematogen (nématogène fondateur). Nouvel (1935, 1936, 1937) has described analogous forms for *Dicyema schulzianum* and *Dicyemennea eledones* and presented additional details about those described by Lameere.

Gersch (1938) failed to find any such forms and was led to deny their existence—attributing the characteristics described by Lameere and Nouvel to faulty interpretation of poorly fixed material. He returned to the concept of the primary nematogen as the earliest form found in the cephalopod.

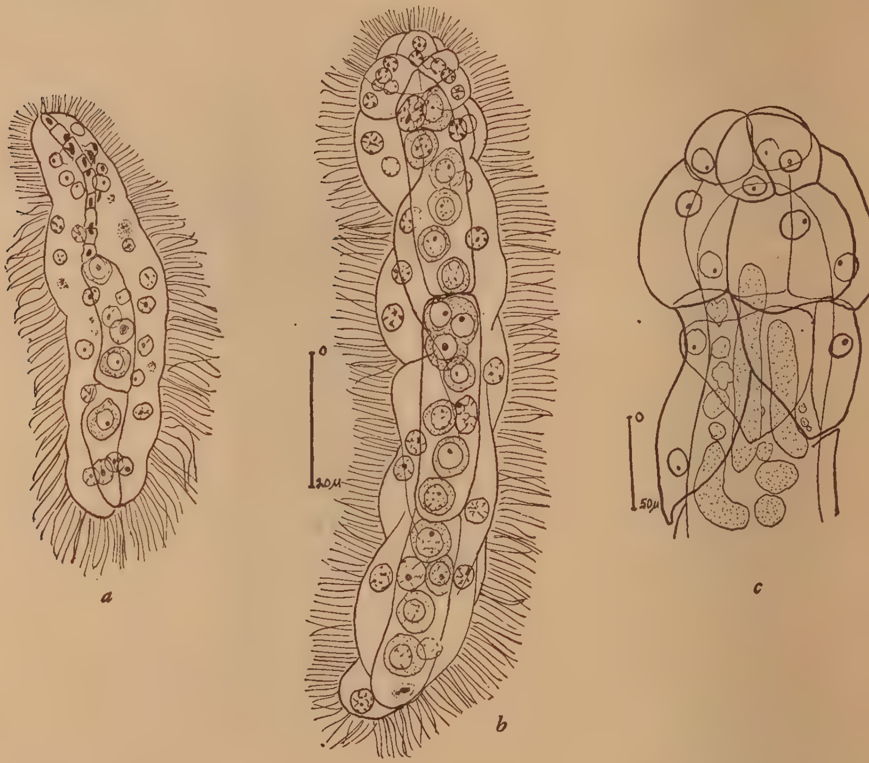

Fig. 2. The stem nematogen. *a.* Larval stem nematogen of *Dicyemennea eledones,* showing a cordon of abortive cells anterior to the two axial cells. *b.* Young stem nematogen of *Dicyema schulzianum,* showing the three axial cells each containing several germ cells. The abortive cells present in younger larvae have been absorbed and are no longer in evidence. *c.* Anterior end of adult stem nematogen of *Dicyemennea eledones,* showing the three parapolar cells. Contained embryos and larvae are lightly stippled. After Nouvel.

Nouvel (1947) reviewed in detail all previous work relating to the stem nematogen phase and presented some new observations of his own.

McConnaughey (1949) described stem nematogens thought to be those of *Dicyema balamuthi* from the coast of southern California.

In view of the extended treatment of the question by Nouvel it is unnecessary to repeat in detail the evidence relative to the existence of the stem nematogen. We can safely conclude that, contrary to Gersch, the forms described as stem nematogens actually do exist in a number of species of dicyemids; and that they are rapidly replaced in young cephalopods by the primary nematogens to which they give rise.

The stem nematogens exhibit remarkable morphological peculiarities (fig. 2) which are of importance for a theoretical interpretation of the morphology and embryology of the other phase of the life cycle. Chief among these is the presence of more than one axial cell. The number of axial cells (three in most known species, two in one) seems constant for each species. They are arranged in linear series in the long axis of the stem nematogen. In larval stem nematogens there are in addition a series of small abortive cells, probably representing additional repressed axial cells, in front of the anterior axial cell. These cells degenerate in place and are engulfed and absorbed by the adjacent somatic cells of the young stem nematogen, leaving no trace in the older individuals. There are also differences in the number and arrangement of the somatic cells between the stem nematogens and the corresponding primary nematogens.

THE PRIMARY NEMATOGEN

The development of the primary nematogen from axoblasts in the stem nematogen or in other nematogens is the most direct and straightforward event in the life cycle of dicyemids. Yet even this has given rise to several points of difference, both in detail and in interpretation, between different authors. As the actual course of embryonic development is slightly more complicated in most members of the genus *Dicyemennea* than in *Dicyema*, the development of the vermiform larva in *Dicyema* will be outlined first. This will be followed by a discussion of the additional features characteristic of most species of *Dicyemennea*.

Development of the Vermiform Larva in the Genus Dicyema

Multiplication of axoblasts.—The germ cells or axoblasts of stem nematogens and primary nematogens multiply in the axial cell by mitotic divisions. The daughter cells are equal in size. The spindle is broad and, though converging somewhat toward the ends, does not come to a definite point. No centrosomes have been found. The chromosomes are very small and too clumped together to enable one to make satisfactory counts. Gersch (1938) described and figured for *D. typus* a stainable ring fibril between the two daughter cells that he claimed represented the remains of the spindle. He described also similar rings following cell divisions at various other points in the life cycle. Other authors have not mentioned this fibril.

Early cleavages.—Even at the first cleavage stage the difference between an axoblast entering into the formation of a vermiform embryo and one that is simply dividing is evident. The axoblast enlarges, and the first cleavage results in slightly unequal daughter cells that adhere to each other along a rather broad plane. Hartmann (1906) believed that the unequal size resulted from different growth rates of the daughter cells after division. Other authors (Whitman, 1883; Lameere, 1919; Gersch, 1938) stated that the daughter cells are unequal from the start. The latter view is correct, as the inequality is sometimes evident while division is still in progress (fig. 3, *a–d*).

The larger of the two cells remains quiescent while the smaller one and its daughter cells continue to divide. The embryo as a whole also increases in size during this time. The cells derived from the smaller blastomere progressively envelope the larger cell which is the mother cell of the future axial cell and all the reproductive cells.

Chromatin elimination.—During the period of early cleavages some small deeply staining masses of chromatin are eliminated from the embryo. They can be seen either still in contact with the embryo or lying near by in the axial cell of the parent nematogen, generally near the anterior end in early stages, though they may occur on all sides of it. They are soon absorbed and usually are not in evidence by the time the larva has become fully developed and ciliated.

Hartmann (1906) first studied these and gave an account of their origin, showing them to be formed by an abnormal mitotic division of one of the embryonic cells, one part consisting of the eliminated chromatin similar in appearance to a polar body, the other retaining nearly all the cytoplasm. He considered this an infrequent abnormal occurrence which any of the cells of the developing embryo might experience. He further asserted that it occurred in larvae from some individual cephalopods and not in those from others, indicating that it might possibly be a pathological reaction related in some way to the condition of the host.

Lameere (1919) gave a very different account and interpretation of this phenomenon. According to him, the large future axial cell shortly before it is wholly enveloped by the somatic cells and before it forms the first germ cell, undergoes an unequal division, eliminating a tiny cell resembling a polar body. This may simply degenerate or itself redivide once or twice so that from one to four of these small abortive elements result. The axial cell itself does not give rise to any more, and, according to Lameere, not more than four of these bodies are ever found associated with an embryo.

Bearing in mind the structure of his recently discovered stem nematogen, he maintained that these small elements in reality represent rudimentary second and third axial cells together with their primary germ cells, so that the embryonic development of the vermiform larva reflects the structure of the stem nematogens but with two of the axial cells aborted—only one developing as a definitive axial cell.

This conclusion rested on the following points: 1. The abortive elements are actually derived from an early division of the large central cell of the embryo, not from any of the somatic cells as Hartmann thought. 2. The phenomenon is general rather than a rare pathological event as Hartmann thought. 3. The number of abortive elements is consistent with the number of extra axial cells in the stem nematogen. 4. They are not formed at any other stages during the life cycle.

Gersch (1938) in his account of the embryology made no mention of these small elements.

Points 3 and 4 of Lameere do not hold true. I have observed frequently more than four of these elements associated with a single vermiform embryo and have also noted their formation by young infusoriforms. This does not necessarily invalidate Lameere's general interpretation of them. Nouvel (1936, 1937) showed that larval stem nematogens have a number of abortive cells in the anterior region which seem without doubt to represent a further number of repressed axial cells, so that the actual number of these elements may not be as significant as Lameere thought. That the contents of the urn of the infusoriforms are homologous to the axial elements of vermiform stages seems well established, hence it is not surprising that similar aborted elements might also be formed during the embryology of the infusoriform.

The formation of these elements appears to be a more constant and normal feature of the embryology than Hartmann thought, but whether Lameere's interpretation of their significance is correct is open to question.

These chromatin granules are found outside the embryos from very early cleavage stages, whereas true aborted axial cells are found within the embryos in larval *Dicyemennea* and in stem nematogens, at a somewhat later stage of development. In developing infusoriforms similar chromatin granules are derived from chromatin eliminated from only part of the blastomeres at the time of the second or third cleavages. These facts suggest another interpretation.

Goldschmidt and Lin (1947) have interpreted chromatin elimination in cell-constant animals as a phenomenon associated with the early cessation of cell divisions of the somatic cells. It has been shown in nematodes that only the sex cells, which retain almost unlimited capacity for further divisions, do not show the phenomenon, whereas the cells giving rise to the soma show early heteropycnosis of the chromosomes leading to elimination of a part of the chromatin.

The dicyemids are a classic example of cell-constant animals. The somatic cells undergo only a very limited number of divisions in the embryo, and further growth is only enlargement and differentiation of cell elements already present so that the adult consists of a small number of giant cells.

Chromatin elimination takes place during the early cleavage stages of both vermiform and infusoriform larvae but not from embryonic infusorigens of corresponding stages of development. This is very suggestive, because the infusorigen is the only stage in which there is no cell constancy, all of the cells of the individual being reproductive cells. The infusorigen does, furthermore, eliminate the paranucleus at the beginning of its formation (see p. 313). This body is here interpreted as equivalent to the small abortive second axial cell of larval *Dicyemennea*.

The formation of aborted axial cells by vermiform embryos, which in late stages of their regression give rise to pycnotic elements resembling the fragments of chromatin formed by true chromatin elimination, may sometimes complicate and confuse the picture. This is probably responsible for the diversity of opinion of earlier writers with respect to the origin of these bodies.

Formation of the first axoblast (fig. 3, *i*, *j*, *k*).—The large inner cell soon becomes wholly enveloped by the smaller somatic cells and the embryo begins to elongate, first assuming a pyriform shape. The calotte constitutes the broad end, as Whitman (1883) pointed out, and the embryo narrows posteriorly. The large internal cell divides into two unequal cells, of which the smaller has denser cytoplasm and lies posterior in position. The larger anterior cell is the definitive axial cell of the developing larva. Its nucleus becomes the axial nucleus and undergoes no further divisions. The smaller posterior cell is the first germ cell or axoblast. It promptly invades the axial cell and undergoes a mitotic division. In many species one of the daughter axoblasts migrates forward around the axial nucleus so that in larvae at this stage we find typically in the axial cell one large free nucleus, the axial nucleus, and

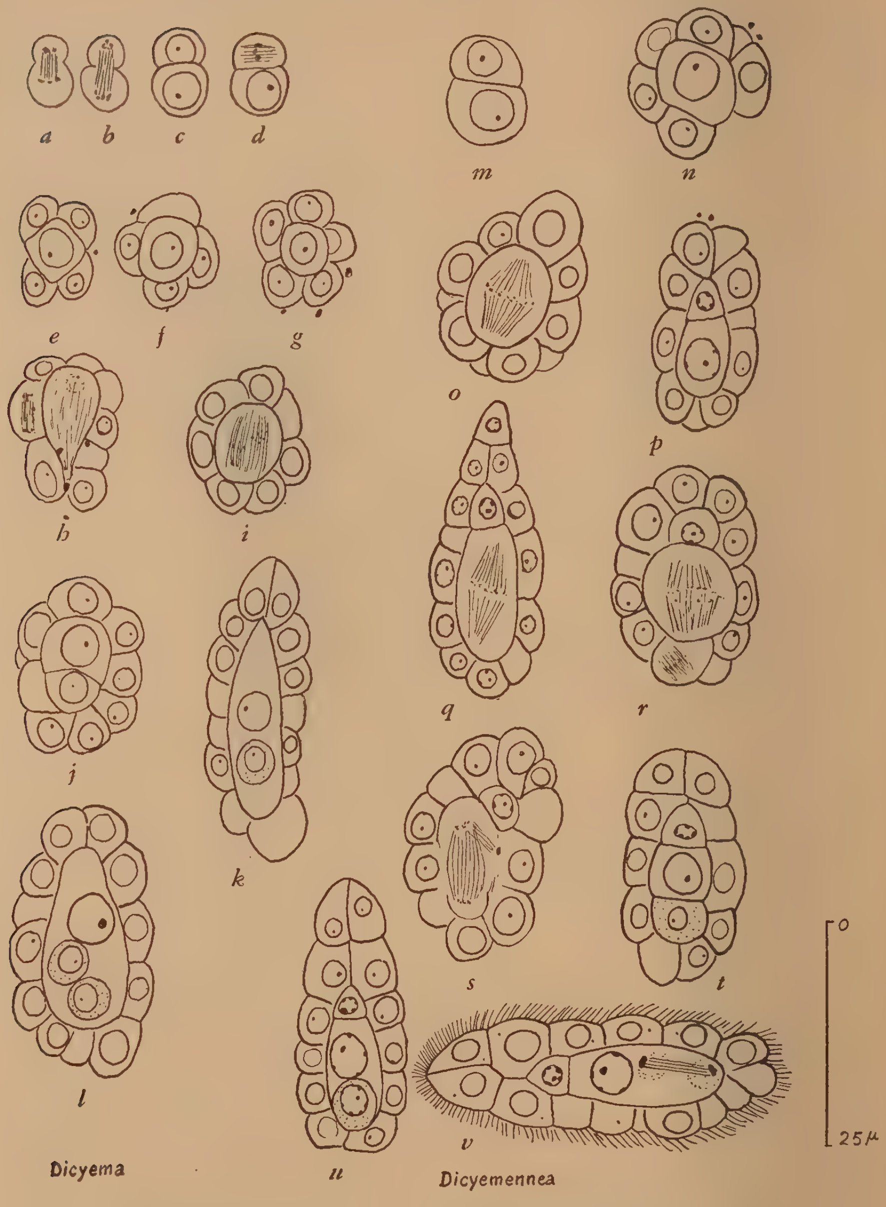

Fig. 3. Embryology of the vermiform larvae of *Dicyema* and *Dicyemennea*. *a–l*, *Dicyema balamuthi*; *n–q*, and *s–v*, *Dicyemennea abelis*; *m* and *r*, *D. californica*.

Dicyema: *a–c*. First cleavage of an axoblast at the beginning of the formation of an embryo, showing the inequality of the blastomeres. *d*. Beginning of second cleavage of the smaller (somatic) cell. *e*, *f*, *g*. Optical sections of young embryos in which the somatic cells have almost completely enveloped the central cell. Some chromatin elimination has taken place. *h*. Optical section of an embryo beginning to elongate. This embryo seemed to have just given off an abortive element from the axial cell, supporting Lameere's thesis that abortive elements may be formed in this manner. Other granules of eliminated chromatin are, however, already around much earlier embryos before two axoblasts, one anterior and one posterior to the axial nucleus. All further axoblasts of the larva are derived from these.

Straightforward as this development is, diverse accounts of it have been given.

Van Beneden (1876) believed that the axoblasts arise spontaneously *de novo* in the axial cell, not from division of previous cells. Whitman (1883) showed that axoblasts do not arise *de novo*. He gave an essentially correct account of the origin of the first germ cell but was not sure whether it was actually cut off from the axial cell at first, later invading it, or if simply formed endogenously by condensation of denser cytoplasm around one of the nuclei of the two-nucleated axial cell following mitosis without cell division. He also thought the second axoblast was derived from the axial nucleus by a second division, though he had not been able to trace its origin definitely.

Hartmann (1904) correctly described the derivation of the second axoblast from the first rather than from a second division of the axial nucleus. He pictured a heteropolar spindle in the first division, the germ cell going to the small (posterior) end, which he mistook for the anterior end.

Lameere (1916) described the division of the nucleus of the internal cell as occurring with a heteropolar spindle, forming two nuclei of different sizes but without any division of the cell body. Vacuolization of all the cytoplasm except that immediately around the germ cell nucleus was said to be responsible for the isolation of the axial nucleus and of the germ cell within the axial cell. Later (1919) he corrected this, having observed that the first division resulted in two separate cells followed by the invasion of the axial cell by the first germ cell. The heteropolar spindle was again pictured.

Gersch (1938) confused the problem by returning to the concept of endogenous formation of the first axoblast. He maintained that what Hartmann (1904) and Lameere (1919) took for a cell wall between the two was in reality simply a ring fibril, a remnant of the spindle plate, and that there was no separation of the first germ cell followed by its intrusion into the axial cell.

I have examined a very large number of embryos in early stages of development in several species and can say definitely that Gersch's account is erroneous in this respect. I have not observed any clear-cut cases of the heteropolar spindle as yet but I am not prepared to say that it may not occur in some species in view of the very clear statements and figures of Hartmann and Lameere about it.

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any indication of a division of the central cell. *i.* Metaphase of the division of the central cell. *j.* Optical section of a larva after completion of the division of the central cell, showing the definitive axial cell and a smaller posterior cell representing the primary germ cell or first axoblast. *k.* Optical section of young larva in which the first axoblast has invaded the axial cell. *l.* Optical section of larva showing the two axoblasts resulting from mitosis of the first axoblast, before the migration of one of them to a position anterior to the axial nucleus.

Dicyemennea: m. Two-celled embryo. *n.* Optical section of a young embryo, the central cell not wholly enveloped by somatic cells. Granules of eliminated chromatin present at the periphery. *o.* Optical section of young embryo showing the first division of the large central cell. *p.* Optical section of larva after first division of the large central cell. *q, r.* Optical sections showing second division of the large internal cell. *s.* Late anaphase of second division of the internal cell. In this embryo some chromatin seemed to have been eliminated, at the time of this division, from the nucleus destined to become the axial cell nucleus. This has not been confirmed in other larvae and is probably not a general phenomenon. *t.* Optical section after completion of the second division of the internal cell, showing a row of three cells axial in position. *u.* Optical section of larva showing the invasion of the definitive axial cell by the primary germ cell. *v.* Optical section showing the first division of the primary germ cell.

THE ABORTIVE SECOND AXIAL CELL IN LARVAL DICYEMENNEA

(Fig. 3, *m–v*)

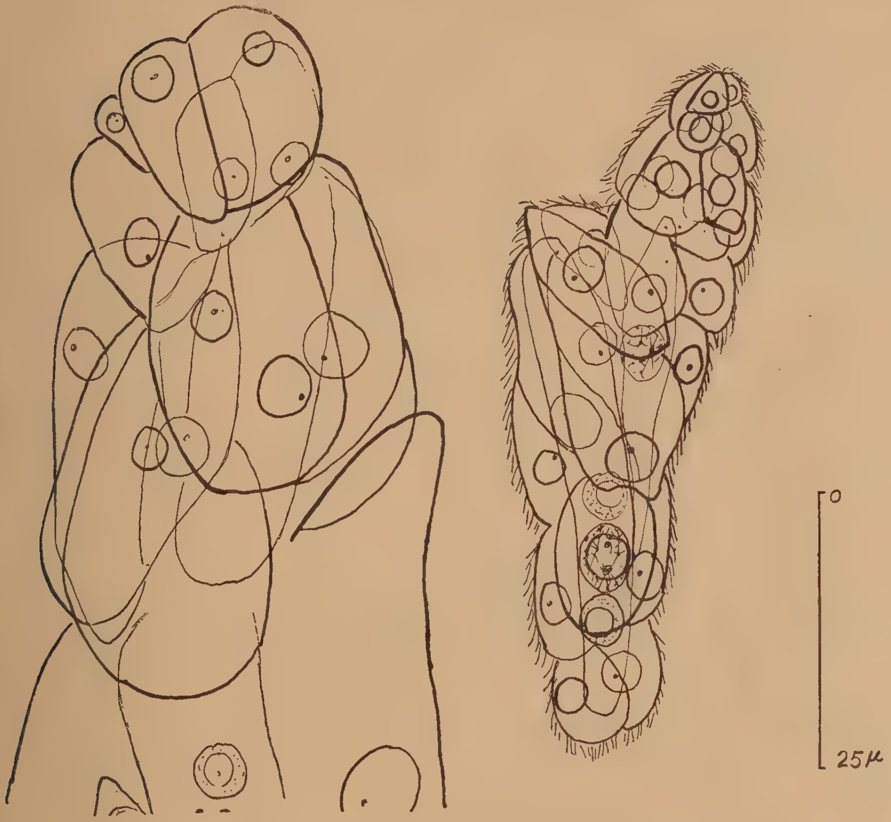
The embryology of the vermiform larvae of most species of *Dicyemennea* differs from that of *Dicyema* in one important respect, which for some reason was entirely overlooked until 1938 when Nouvel published a preliminary note regarding it.

In vermiform embryos of most species of *Dicyemennea* the large internal cell, after it is enclosed by the smaller somatic cells, undergoes two unequal divisions instead of one as in *Dicyema.* The first cuts off a smaller cell that comes to lie anterior to the axial cell in the region of the metapolar cells. The second cuts off a similar but slightly larger cell posterior to the axial cell. Thus we have in the young embryos a row of three internal cells very suggestive of the condition of some stem nematogens (fig. 3, *t*). The largest of the three, the central one, becomes the definitive axial cell of the larva. The posterior one, as in *Dicyema,* invades the axial cell and constitutes the first axoblast. The small anterior cell, however, remains in place anterior to the axial cell between the metapolar cells, in some species near their basal ends, in others shoved well forward against the base of the propolar cells. It degenerates in place and is absorbed, leaving no trace in the adult.

In the last stages of degeneration this cell is often ingested by the dorsal metapolar cell, where it is rapidly digested within a vacuole. In *D. brevicephala* it passes into one of the propolar cells. In any case it has usually, though not invariably, completely disappeared by the time the larva escapes from its parent nematogen, or soon thereafter. *Dicyemennea gracile* (Wagener) is the only species of *Dicyemennea* in which no small abortive cell is formed during the early development of the vermiform larva.

The position and staining characteristics of this small cell suggest that it represents a second axial cell, the development of which is ordinarily repressed. An unexpected confirmation of this view was found in the case of one large abnormal nematogen with a hereditary malformation, in which the factors responsible for arresting cell division and development in the anterior region evidently suffered delay. The nematogen and two of its contained larvae showed an extra ring of metapolar cells in the calotte. The small abortive cell, present in its usual form in most of the embryos, had in these elongated and grown back, developing into an unmistakable axial cell, pushing the fore end of the regular axial cell to one side so that the larva bulged out to give almost the appearance of fused lateral twins (fig. 4).

The embryology of vermiform larvae of *Dicyemennea* reflects the condition of the stem nematogen, and probably of the ancestors of the dicyemids, more closely than does that of *Dicyema.* A small suppressed second axial cell is formed as a constant feature in most species. In *Dicyema* this is omitted, together with the fifth metapolar cell. In rare cases larvae have been found within *Dicyema* nematogens in which these were present, making the larvae typical *Dicyemennea.* It seems that the responsible factor is probably an alteration in rates of embryonic development so that the factor or factors responsible for arresting cell division in the region of the calotte are operative slightly earlier in *Dicyema.* The transition apparently can be made in one step.



a *b*

Fig. 4. *a.* Calotte of very abnormal nematogen of *Dicyema balamuthi* (?) showing almost complete reduplication of the metapolar set of cells. *b.* Abnormal vermiform larva from this nematogen, showing the same anomaly. The abortive second axial cell has here grown back and developed into a clear-cut axial cell but without any axoblasts. The anterior end of the definitive axial cell has been pushed to one side, causing a bulging. It is noteworthy that the abnormally developed calotte should be accompanied by the appearance and unusual development of this rudimentary second axial cell not usually found in *Dicyema.* Other more normal appearing larvae contained in this same nematogen were still abnormal for *Dicyema* in having five, instead of four, metapolar cells and in having a small second axial cell present in the form characteristic for *Dicyemennea.* These larvae and any adults that might develop from them would, by themselves, be indistinguishable from normal individuals of *Dicyemennea.*

Later Development of the Larva

After attaining their definitive cell number and organization the larvae continue to to grow simply by enlargement and elongation of existing cells. No further cell divisions take place except for multiplication of the axoblasts, which begins about the time the larvae escape from the parent nematogen. They become ciliated and active while still within the axial cell of the parent, finally escaping through the side of the body, leaving no scar. The larva fixes itself to the renal tissue of the host and grows into a mature nematogen which produces further generations of larvae. This continues until the renal organs are thickly populated by parasites.

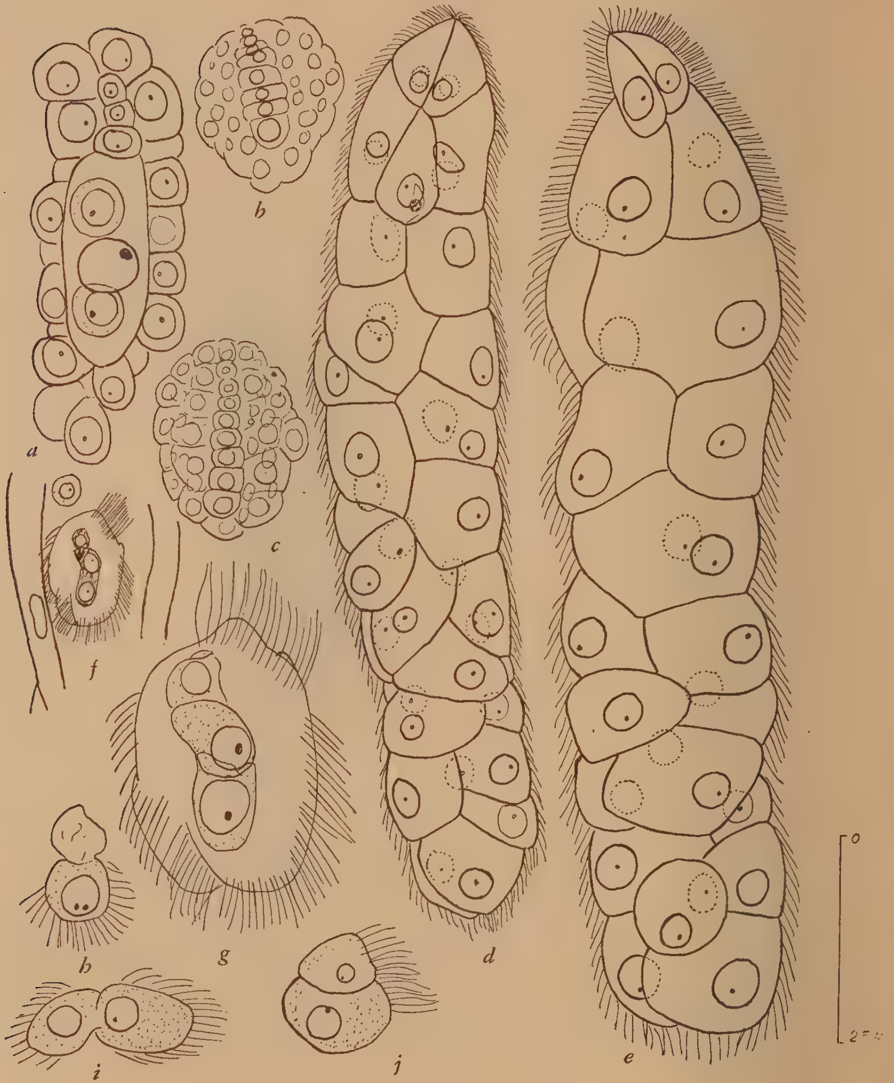


Fig. 5. *a*. Abnormal larva of *Dicyemennea granularis* with three abortive axial cells anterior to the definitive axial cell. *b, c*. Very unusual larvae of *D. granularis* with more than the normal number of cells. Internally there is a row of cells, axial in position, decreasing gradually in size toward what is taken for the anterior end. *d, e*. Fully formed larvae of *D. californica* without any axial cell, and with abnormal calotte in one case (e). These larvae had already escaped from the axial cells of their parents and were free-swimming. *f*. Unusual body found in axial cell of a mature nematogen of *D. abelis*. *g*. Detail of body shown in *f*. *h, i, j*. Other unusual cells scattered near by in the axial cell of the same nematogen. These appear to have been derived from the disaggregation of a fully formed larva before its escape from the axial cell.

ABNORMALITIES OF VERMIFORM STAGES

In rare instances abnormalities occur in the vermiform individuals that throw light on related normal conditions or that may be very puzzling when first encountered. Some of those encountered during this study are listed here.

1. Abnormal numbers of cells in the calotte have already been discussed in connection with Wheeler's genus *Dicyemodeca* (McConnaughey 1949).

2. In one instance, a vermiform larva of *Dicyemennea granularis* had three small abortive axial cells anterior to the definitive axial cell instead of the usual one. This is reminiscent of the conditions described by Nouvel (1936, 1937) for very young stem nematogens (fig. 5, *a*).

3. One large *D. granularis* nematogen of normal appearance contained four very exceptional larvae with plump rounded bodies composed of many more than the usual number of somatic cells arranged partly in longitudinal rows, and with a cordon of eight or nine small cells axial in position and diminishing in size anteriorly. Several other cells also seemed to be in the interior of the body rather than constituting part of the surface. These larvae might be interpreted as reversions almost to an orthonectid condition (fig. 5, *b*, *c*).

4. In rare instances larvae are formed with no axial cell. They may attain full development, become ciliated, and escape from the parent nematogen. It is not known whether this condition is a result of an accidental separation of the blastomere representing the axial cell from the rest of the embryo in the earliest stages of cleavage, or if this cell may have been present in the young embryo and failed to develop further. The fact that in one instance a small rudimentary axial cell similar to that normally present in larval *Dicyemennea* was present suggests the latter alternative for at least some cases. No adults exhibiting this abnormality have been found (fig. 5, *d*, *e*).

5. In rare instances vermiform (also infusoriform) larvae after reaching full development within the axial cell of their parent, fail to make their escape. Instead, they degenerate in place and undergo complete disaggregation and absorption within the parent organism. During this disaggregation their cells, or groups of cells, may become scattered some distance up and down the axial cell, forming bizarre-appearing ciliated bodies like peculiar ciliates or other organisms wholly foreign to the normal contents of the axial cell. This disaggregation usually affects only one or two larvae in a given nematogen; others in the same state of advancement and even right beside them in the axial cell remain perfectly normal and unaffected (fig. 5, *f*–*j*).

6. Several dicyemids from one cephalopod exhibited degenerative changes in one or two of their somatic cells. The cytoplasm of the affected cells took a strong basophilic stain in sharp contrast to the other cells, and the nuclei appeared pycnotic. Usually only one cell in an individual was so affected, the others appearing perfectly normal.

THE RHOMBOGEN PHASE

When the renal organs of the cephalopod have become heavily populated by the parasites, a change of phase occurs in many or most of the individuals present. They cease producing vermiform larvae and instead give rise to a few peculiar, reduced individuals called infusorigens that never leave the axial cell of their parent. The infusorigens proliferate a number of large egg cells that come to lie free in the axial cell of the rhombogen and from which a very different sort of larva, the infusoriform, develops.

During the period of transition numerous secondary phenomena occur in the transforming nematogen so that the rhombogen differs in its own right from the nematogen in addition to possessing a changed type of reproductive element and larvae.

Vermiform larvae liberated during this period, upon attaining maturity usually form infusorigens and infusoriforms directly, without previously functioning as nematogens. These are termed primary rhombogens. Those resulting from the transformation of older nematogens are called secondary rhombogens. There has been little agreement between different authors either on the details or on the interpretation of the phenomena attendant upon the change of phase.

For convenience, these changes are divided into several categories and considered separately, as follows:

Somatic changes differentiating the rhombogen from the nematogen.
- (a) Size and proportions.
- (b) Accessory nuclei in the somatic cells.
- (c) Verruciform cells.

Changes in the contents of the axial cell.
- (a) Degenerative changes leading to destruction of germ cells.
    - (1) Degeneration in place in the axial cell.
    - (2) Entrance of germ cells into the somatic cells and their absorption there.
    - (3) Temporary lodgment of germ cells between the axial cell and the somatic cells.
    - (4) Ingestion of some germ cells by other germ cells.
    - (5) Origin of free nuclei other than the paranuclei.
- (b) Changes leading to the formation of the infusorigen.
    - (1) Fusiform and binucleate axoblasts.
    - (2) Enlarged germ cells—mother cell of the infusorigen.
    - (3) Elimination of the paranucleus.

SOMATIC CHANGES

Size and proportions.—Rhombogens of many species tend on the average to be somewhat longer and wider than the nematogens, though this is by no means invariable. The elongation does not affect the propolar cells but may affect the other cells of the cephalic swelling so that this region becomes elongated and narrower, no longer presenting a swelling (fig. 6, *a*). This phenomenon is not constant even in the same species and is not invariably associated with the rhombogen condition. In a few species, very short thick rhombogens are found, much shorter than the corresponding nematogens. In most species the rhombogen seems more robust or heavy-set than the nematogen.

Accessory nuclei in the somatic cells.—The most conspicuous somatic change and the one that can be most surely relied upon to indicate a change of phase is the appearance of accessory nuclei in some of the somatic cells of the trunk. This takes place through an amitotic division or budding of the nuclei in these cells. The divisions are usually very unequal. Sometimes redivision or renewed budding

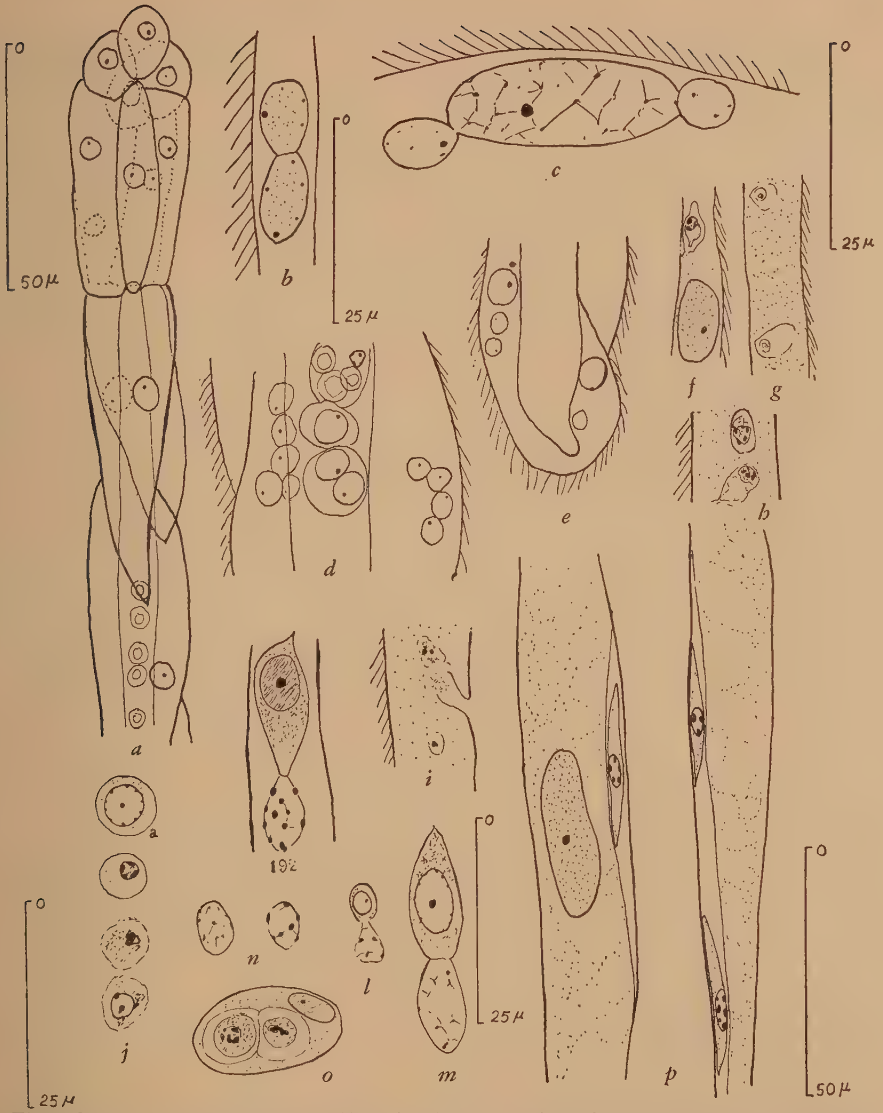


Fig. 6. Secondary phenomena attending the change of phase from nematogen to rhombogen. *a.* Anterior end of young rhombogen of *Dicyemennea abelis* showing elongation of meta and parapolar cells. *b, c.* Amitotic division of the nucleus in somatic cells of transitional individuals of *D. adscita. d.* Part of trunk of rhombogen of *Dicyema acciaccatum* with little chains of nuclei in the somatic cells. *e.* Caudal end of rhombogen of *D. acciaccatum* showing accessory nuclei in somatic cells separated from the main bodies of the original nuclei. *f, g, h, i.* Parts of somatic cells from transitional individuals of *D. balamuthi* showing digestion and degeneration of invading axoblasts. *j.* Stages in the degeneration of axoblasts in place in the axial cell of a transitional individual of *D. balamuthi. k, l.* Elimination of nucleus-like body from enlarged germ cells in *D. balamuthi.* These bodies are apparently not formed by any direct division of the nucleus of the cell. This is what Hartmann (1906) termed the chromidial origin of accessory nuclei. *m.* Similar expulsion of a nucleus-like body from a small axoblast. *n.* Free nucleus-like bodies in the axial cell of a transitional individual, probably derived from axoblasts in the above manner. *o.* Enlarged germ cell in transitional individual of *Dicyemennea californica,* containing two smaller axoblasts in the course of digestion in vacuoles in its cytoplasm. *p.* Part of trunk of an early transitional individual of *Dicyema apollyoni* showing germ cells lodged between the axial cell wall and the inner walls of the somatic cells.

occurs before the first bud is completely separated from the parent nucleus, so that little chains of three or four or more incompletely separated nuclei may be formed (fig.6, *b–e*).

The presence of these accessory nuclei makes it difficult to obtain reliable cell counts on rhombogens. They also persist and may be seen in secondary nematogens where they constitute one of the criteria for recognizing the latter.

The time of onset of these amitotic nuclear divisions in the somatic cells does not always correspond precisely with the first noticeable changes in the reproductive elements of the axial cell. In some species of *Dicyema* in particular it may precede these changes so that accessory nuclei can often be found in the epithelial cells of mature nematogens.

Wheeler (1897) and Hartmann (1904) observed these supplementary nuclei and thought that they were derived from germ cells that passed into the somatic cells and were digested there, leaving only the nucleus.

Lameere (1918) stated that he had never observed this supposed passage of germ cells into the peripheral cells, and, from the similarity of the accessory nuclei to the regular ones present, concluded that they were formed by unequal amitotic division of the latter. Later (1919), after finding evidence of the passage of germ cells into the somatic cells, he reversed his opinion, deciding that the supplementary nuclei were derived from immigrant germ cells after all, though he stated that it was a very remarkable circumstance that the somatic cells should be able to adopt nuclei not their own and use them as such.

Nouvel (1933, 1934) pictured the entrance of germ cells into somatic cells, particularly the uropolars and verruciform cells, and their subsequent digestion there.

Gersch (1938) found amitotic divisions of somatic nuclei and considered them degenerative changes preceding the death of the old rhombogens. Nouvel (1947) agreed with Lameere that these nuclei are derived from axoblasts that have invaded the peripheral cells and whose cytoplasm has there been digested. He wrote, "L'origine des noyaux accessoires de la cellule axiale sera traitée plus loin [chapitre V]. Il paraît bien que ceux des cellules périphériques ne résultent jamais d'une division directe ou indirecte de ces cellules."

I have many times observed the presence of axoblasts in various stages of degeneration and absorption in the somatic cells of the trunk (fig. 6, *f–i*), particularly in individuals transitional between the nematogen and the rhombogen phases. These axoblasts, however, are always in vacuoles, and all stages of their degradation, from whole ones just entered to small deeply staining pycnotic nuclear fragments, can be found. There is no evidence that their nuclei ever persist as accessory nuclei of epithelial cells into which they have entered. The accessory nuclei of these cells are derived from the epithelial cell nuclei themselves by amitosis or buddings. These are to be considered degenerative changes, as Gersch (1938) maintained. The change occurs, however, not as a final pathological change immediately preceding the death of old rhombogens as Gersch thought, but at the time of, or even slightly before, the onset of the rhombogen phase. Furthermore, in different species it takes place characteristically in slightly different ways and begins in different cells. Thus in *Dicyemennea granularis* the first accessory nuclei are normally formed in the parapolar and anterior diapolar cells after the nuclei of these cells become irregular and polymorphic in shape. In several other species accessory nuclei are first formed in the diapolar cells more posterior in position along the trunk and seem to be simply budded out and pinched off from the cell nucleus without its first undergoing marked changes in shape.

Verruciform cells.—Nouvel (1933) described the formation of verruciform cells in *Dicyema clausianum* and stated that: "L'un des premiere phénomènes qui marquent la transformation du nématogène primaire en rhombogènė (phénomènes rhombogéniques, Lameere) est précisément la formation des verrues ..."

This statement possibly is true for the majority of individuals of some species but is certainly not a general or invariable criterion of the transition of phase. Some species do not form verruciform cells at any time. In others the two caudal cells, the uropolars, are typically verruciform in character in both phases. The single granular uropolar cell of the stem nematogen described by Lameere is of this character. In several species of *Dicyemennea* I have noted verruciform cells on young nematogens as well as older ones and rhombogens.

The formation of verruciform cells seems to be a phenomenon associated with intense activity within the axial cell in the production of both vermiform and infusoriform embryos. Because the accumulation of nutritive reserves in the somatic cells preceding the active rhombogen activity is marked, and because the production of infusoriforms seems as a rule to proceed at an accelerated rate compared with that of the vermiform larvae, it may be true that verruciform cells are found more often on early rhombogens than on other stages, in those species that ordinarily have them.

CHANGES WITHIN THE AXIAL CELL

Degenerative changes leading to destruction of germ cells.—Mature nematogens, just before the transition to the rhombogen phase, often have a very large number of axoblasts in the axial cell. The majority of them are eventually lost through degeneration and absorption, only a few persisting, some becoming the mother cells of the infusorigens.

The degeneration is first evidenced by altered staining reaction of the cell. The cytoplasm becomes paler and more eosinophilic. The nucleus shows progressive clumping of the chromatin, which forms deeply staining masses at the periphery of the nucleus. The nucleus itself becomes smaller, moves to the periphery of the cell, and eventually disassociates into small fragments that may persist for a time after most or all of the cytoplasm has been absorbed. During the later stages of this degeneration the axoblasts is inclosed in a digestive vacuole in the axial cell.

The appearance of these cells during their digestion is varied, especially in the genus *Dicyema,* and at one time led Lameere (1914) to believe that it was a process of spermatogenesis. His article, *Le mâle des Dicyémides,* was based upon this interpretation. Later (1918) he realized his error and recognized that what he had taken for males were simply small groups of degenerating axoblasts in various stages of degeneration, and that what he had taken for sperm were the last pycnotic chromatin remnants of their nuclei.

Some of the axoblasts become amoeboid and invade the somatic cells, where they undergo digestion in vacuoles in the same manner as in the axial cell. When verruciform cells are present the axoblasts enter these most often, though they sometimes invade other trunk cells as well.

Less frequently a number of them may, instead of being digested in place or passing directly into an epithelial cell, become lodged between the axial cell and the inner wall of a somatic cell. Here they assume a flattened irregular or elongate, fusiform, shape and may persist for some time. Koeppen (1892) described certain amoeboid cells that he thought wandered out of the dicyemid and might perhaps be amoeboid sperm, entering others and fertilizing them. He also described muscular elements. It seems probable that what he observed was the passage of axoblasts into somatic cells and the lodgment of some between the axial cell and the somatic cells. When thin and elongate in shape these latter might easily be taken for muscle cells, and their position at this time, if we consider the axial cell endodermal as most earlier writers did, is actually mesodermal as might be expected of muscular elements (fig. 6, *p*).

A few instances of axoblasts being engulfed and digested by larger germ cells have also been observed (fig. 6, *o*).

In some cases nucleus-like bodies are eliminated from some of the germ cells in the manner described by Hartmann (1907), which he termed the chromidial origin of accessory nuclei (fig. 6, *l–n*).

Changes leading to the formation of the infusorigen.—Frequently in early transitional individuals, a small number of the axoblasts present are slightly larger than the average and possess two nuclei. Gersch (1938) and others have noted these binucleate axoblasts, though without correlating them with any particular phase of the life cycle, and have believed them simply the result of abnormal mitosis in which the cytoplasm failed to divide after nuclear division.

The uniformity with which they appear, particularly evident in young primary rhombogens where the end members of the row of axoblasts on either side of the axial nucleus are commonly binucleated (McConnaughey, 1949, pl. 2, fig. 24), suggests that the phenomenon may have a more fundamental significance. Occasionally a cell may be found in which the two nuclei appear to be undergoing fusion. Slightly older individuals show the presence of enlarged uninucleate cells, some of which become fusiform in shape with long drawn out, sharply pointed ends (fig. 7, *b*). It seems probable that some of the smaller ordinary axoblasts also become fusiform, for intergradations between these and the fusiform cells can also be found. The number of fusiform cells present often far exceeds the largest number of binucleate axoblasts seen or the number of infusorigens later formed. Many of them are lost through degradation in the axial cell in a manner comparable to that of the ordinary axoblasts. Sometimes the cytoplasm appears to be digested away, leaving only the empty cell wall and a somewhat enlarged nucleus which fills it so that the whole cell takes on the appearance of an accessory free nucleus in the axial cell. This is more often observed at the end of the rhombogen phase at the time partly formed infusoriforms are disaggregating than at the beginning.

That the binucleate axoblasts actually are precursors of the mother cells of the infusorigens has not been shown. It was suggested on circumstantial evidence and as a possible explanation for the diploid constitution of the infusorigen (Mc-

Connaughey, 1948). If the interpretation of the life cycle here developed is correct this would seem improbable on theoretical grounds as it would involve a reduction of the chromosome number to haploid sometime during the unknown part of the life cycle, as well as during the formation of germ cells by the infusorigen.

It may be, as Gersch believes, that the binucleate axoblasts represent simply another indication of the upset of normal axoblast development attendant upon the change of phase and are merely cells in which cytoplasmic division has failed to follow nuclear division.

The paranucleus.—The first definitive act of the mother cell of an infusorigen is an unequal division with the elimination of a smaller cell, which soon loses all appearance of possessing any cytoplasm and remains in the axial cell of the parent rhombogen as an accessory free nucleus—the paranucleus of Whitman (1883). It is small at first but usually increases in size as the infusorigen matures. In some species, for example, *Dicyemennea californica,* by the time the infusorigen is mature and functional, the paranucleus has attained approximately the same size and appearance as the axial nucleus of the parent rhombogen, from which it may become difficult or impossible to distinguish it with certainty (fig. 7, *e–l*).

Thus, typically, there comes to be in the axial cell of a rhombogen one more free nucleus than there are infusorigens—the original axial nucleus, plus one paranucleus corresponding to each infusorigen.

In some species, especially in certain *Dicyema,* the picture may be complicated by secondary amitotic divisions of the axial nucleus or of one or more of the paranuclei, or by the chromidial formation of free nuclear bodies as described by Hartmann (1906). In such cases the number of free nuclei in the axial cell no longer is equal to the number of infusorigens plus one but exceeds this by an indefinite number.

These secondary phenomena, together with the budding off of accessory nuclei in the somatic cells, have confused the picture to such an extent that some authors have been led to deny that there is any relationship at all between the infusorigens and the free nuclei present in the axial cell.

Gersch (1938) for instance, says: "Wie aber schon Hartmann, Lameere, u. a. gezeigt haben, handelt es sich dabei um Verwechslungen mit den Kernen von Aussenzellen und mit Fragmenten des Axialzellkerns, wie sie in alternden Würmformigen nicht selten verzufinden sind."

It seems odd that Gersch should cite Lameere in support of this point of view, when Lameere himself (1919), after further study of the problem, renounced his earlier position (1918) and gave a detailed account of the origin of the paranucleus corresponding closely to that of Whitman.

It is true that other accessory nuclei sometimes arise in certain species in the manner described by Hartmann (1904), Lameere (1918), and Gersch (1938). But this in no way invalidates Whitman's general thesis about the origin of the paranuclei though it does lessen the value of accessory nuclei as criteria for recognition of secondary nematogens.

In several species of *Dicyemennea* the phenomenon is usually uncomplicated, the true paranuclei being the only accessory nuclei present in the axial cell, and

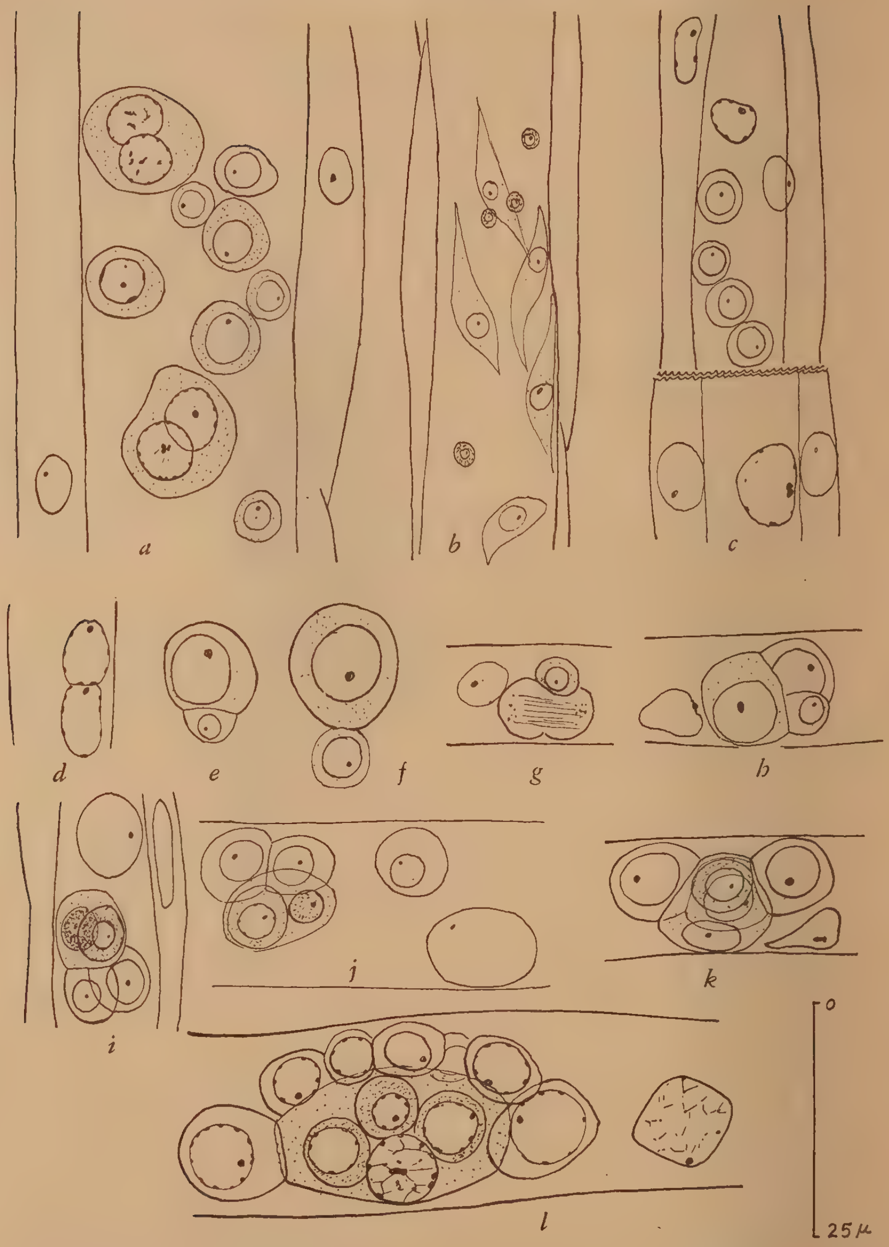


Fig. 7. *a.* Part of transitional *Dicyemennea brevicephala* showing two enlarged binucleate axoblasts. *b.* Part of early transitional *D. granularis* with both normal and enlarged fusiform axoblasts. *c.* Two parts of the trunk of a young *Dicyema balamuthi* containing two free nuclei, presumably derived from a single original axial nucleus by amitotic division. *d.* Part of the axial cell of a young *D. balamuthi* in which the axial nucleus is undergoing amitotic division. *e.* Elimination of a small cell, the future paranucleus, from the mother cell of an infusorigen in a transitional individual of *Dicyemennea californica*. *f.* Slightly later stage of the same. *g.* Very young infusorigen of *D. abelis* showing the second division of one of the cells, and the paranucleus lying

their correlation with the number of infusorigens being perfectly clear. In these species, in transitional individuals whose axial cells are still very crowded with axoblasts and vermiform embryos, the earliest infusorigens, which resemble young vermiform embryos in many respects, can often be most easily spotted by searching carefully in the vicinity of any small paranuclei that may be present.

The significance of the paranucleus will be discussed below as part of the whole question of the role of the infusorigen.

THE INFUSORIGEN

Embryology of the Infusorigen

(Fig. 7, *e–l*)

The first cleavage of the mother cell of an infusorigen, following the elimination of the paranucleus, is unequal. The smaller cell is the forerunner of all the peripheral cells of the infusorigen, which later become egg cells; the larger one gives rise to the axial cell of the infusorigen and the germ cells contained therein.

Contrary to the early vermiform embryo, there is no period of delay before the next division of the larger cell, which is also unequal—the second cleavage of each blastomere occurring at nearly the same time. The young infusorigen then consists of four cells: a large cell that represents its axial cell and undergoes no further division, a small cell that promptly invades the axial cell and from which all the male germ cells of the infusorigen are derived, and two peripheral cells that remain outside the axial cell and are the forerunners of all the egg cells produced by the infusorigen. In some instances it appears that the division producing the small cell destined to invade the axial cell of the infusorigen precedes that which separates the definitive axial cell from the first of the peripheral cells.

There is no elimination of small chromatin granules during the very early development of the young infusorigen as is characteristic of early vermiform embryos.

Both the outer cells and the internal germ cells continue to multiply for a time by ordinary mitosis until the infusorigen consists of a large axial cell containing several germ cells similar to axoblasts in appearance and a number of peripheral cells partly enveloping the axial cell. The envelopment of the axial cell is usually incomplete to an advanced stage, so that in optical section the axial cell of a young infusorigen appears to be surrounded on only three sides by the peripheral cells, the side nearest the axial cell wall of the parent rhombogen usually being exposed. This is in marked contrast to the early vermiform larvae, in which the axial cell is very early enveloped completely by the peripheral cells.

In older mature infusorigens the axial cell appears fully enveloped. There is no differentiation of the body of the infusorigen into calotte and trunk. Instead, from this point on the cells undergo an entirely different course of development.

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close by. *h.* Very young infusorigen of *Dicyema adscita* showing definitive axial cell of the infusorigen. The first peripheral cell of the infusorigen, the first internal germ cell of the infusorigen (still outside the axial cell) and the paranucleus. *i, j.* Young infusorigens of *D. abelis.* The first internal germ cell has invaded the axial cell and the first peripheral germ cell has divided, forming a four-cell stage. The paranucleus lies close by. *k.* Similar young infusorigen in which one of the two peripheral cells has redivided, giving a five-cell stage. *l.* Optical section of a typical young infusorigen of *D. apollyoni* just before the onset of meiotic divisions. The axial cell is not entirely enveloped by peripheral cells. The paranucleus lies nearby in the axial cell of the parent rhombogen.

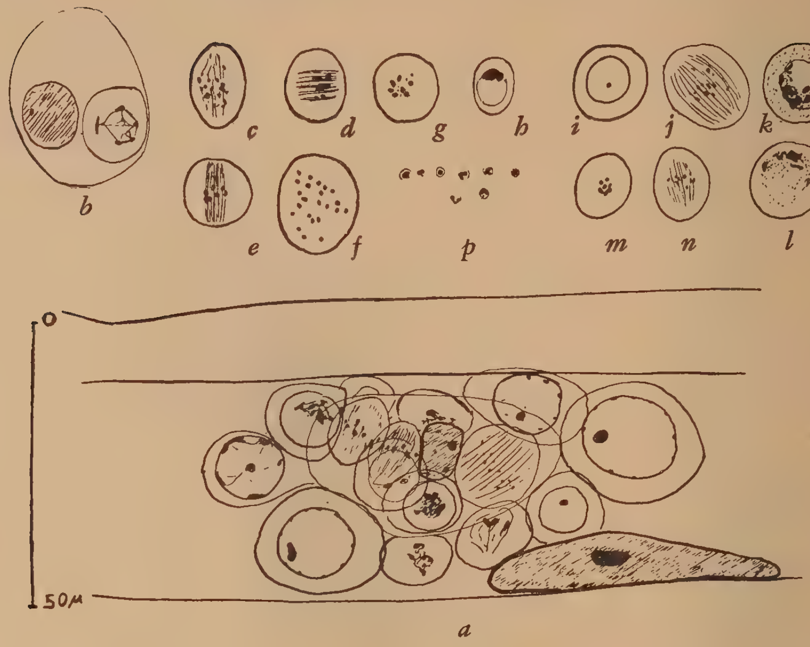

Fig. 8. *a.* Young infusorigen of *Dicyemennea californica* at time of onset of meiotic divisions of some of the cells. Characteristic clumping of the chromatin at one side of the nucleus, on strands of lighter staining material. In cells inside the infusorigen this is followed by reduction divisions leading to sperm formation. In the peripheral cells it is followed by a swelling of the cell as a whole and its nucleus. The reduction divisions of the egg do not occur until after sperm penetration. The paranucleus lies near by. Comparison with the paranuclei of a younger infusorigen shows a progressive increase in size until it becomes very similar in size and appearance to the axial cell nucleus of the parent rhombogen. *b–p.* Internal or male germ cells of the infusorigen: *b. Dicyema balamuthi,* axial cell of an infusorigen and one of its contained germ cells, showing chromatin clumped on light-staining network. *c. Dicyemennea brevicephala,* first meiotic division of one of the germ cells. *d, e. Dicyema apollyoni,* second meiotic division of internal germ cells of an infusorigen. Seven or eight dyads with the appearance of single chromosomes are present on the metaphase plate. *f. Dicyemennea californica,* polar view of metaphase plate of spermatogonial division. At least twenty-three chromosomes can be seen. *g. D. californica,* polar view of male cell in second meiotic division. Eleven or twelve chromosomes can be made out. *h. Dicyema apollyoni,* spermatid. *i–p.* Male cells in various stages from a single infusorigen in a transitional individual of *Dicyemennea californica: i.* Spermatogonium before any changes preceding meiosis. *j.* Spermatogonial division. *k, l.* Clumping of chromatin at one side of nucleus preceding meiosis. *m. n.* Polar and side views of secondary spermatocyte division showing approximately eight dyads on the metaphase plate. The chromosomes and cells of dicyemids are so small that tetrads and dyads could not be distinguished as such, but appeared as just slightly larger chromosomes than those of other stages. *o.* Spermatid. *p.* Group of sperm cells.

MATURATION OF GERM CELLS AND FERTILIZATION

(Figs. 8 and 9)

Some of the axoblast-like cells inside the axial cell of the infusorigen continue to multiply by ordinary mitotic divisions. Rather early, however, the nucleus in others swells up noticeably; its chromatin is gathered near one pole in strands or as small knots of chromatin on strands of lighter staining material, forming a sort of radiating anastomosing network of fibrils. The chromosomes become individualized and the cell undergoes two successive divisions, resulting in smaller cells each time. The smallness and crowding of the chromosomes has made it difficult to get an accurate count of their number but estimates on the clearest cases indicate a reduction in chromosome number by about half during these divisions. After the second division the chromosomes become lumped together in a tight little knot. The cytoplasm is almost all sloughed off and quickly disintegrates. The small tailless sperm lie scattered about near the periphery of the infusorigen and attach themselves to the mature oögonia at or near the point where these are attached to the infusorigen.

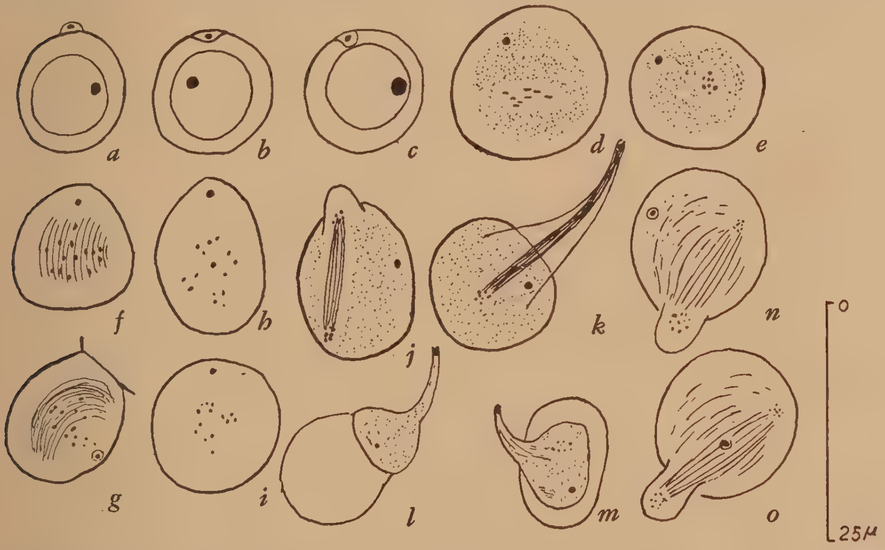

Fig. 9. Fertilization and polar body formation of the egg cells. *a–c. Dicyemennea adscita*, three stages in the penetration of egg cells by sperm. *d, e. D. adscita*, shortly after sperm penetration. The germinal vesicle has broken down and the chromosomes are becoming aligned on a forming spindle—lateral and polar views. *f–i. Dicyema apollyoni*, egg cells showing chromosomes, approximately fourteen in number scattered on the spindle in early anaphase preceding the elimination of the first polar body. *j, k. D. apollyoni*, elimination of first polar body. Seven chromosomes could be seen in the group remaining in the egg cell. *l, m. D. balamuthi*, extrusion of first polar body. In this species the part of the egg containing the chromosomes and spindle appears sharply set apart from the remainder of the cytoplasm during the division. *n, o. D. balamuthi*, extrusion of the second polar body. Each group of chromosomes can be seen to consist of approximately eight or nine chromosomes.

Meanwhile the larger peripheral cells or oögonia have multiplied. Some of them show similar phenomena to the spermatogonia, with a clumping of the chromatin in small knots and strands at one side of the nucleus followed by a marked swelling of both the whole cell and its nucleus. The nucleus possesses a large nucleolus and small granules of chromatin distributed on an achromatic network. It is at this time that the sperm attach themselves to the egg cells.

Shortly before or just after the attachment of the sperm cell, the egg cell detaches itself from the infusorigen and lies free in the axial cell of the parent rhombogen. The sperm penetrates a short distance into the cytoplasm and remains there unaltered while the nucleus of the egg cell loses its membrane, forms a division spindle, and undergoes two rapid successive divisions with the elimination of a polar body from one end of the cell each time. The spindles in these divisions are usually very long, with the two groups of chromosomes at opposite poles of the cell. The first division is generally rapid, the polar body in some species pushing out onto a long stalk-like process. The second division is more frequently found.

In some examples definite reduction by half of the chromosome number has been established, though the smallness of the chromosomes makes exact counts difficult even in the large egg cells. However, a few clear cut cases of reduction to half, plus a number of estimates of approximate number showing a reduction by approximately half, clearly indicate that these actually are meiotic divisions.

After the elimination of the second polar body, both the egg nuclear elements and the sperm reconstitute separate nuclei so that the egg has two pronuclei—the usual male and female pronuclei. During the early stages of reconstitution of the female pronucleus several nucleus-like vesicles are often formed around separate chromosomes or groups of chromosomes so that the egg cell may temporarily appear to have several nuclei of various sizes. These unite quickly, however, and it is far more usual to find eggs with two well-formed pronuclei than the earlier stages with several vesicles. Caullery and Lavallee (1912) found the same condition of early formation of several vesicles by the female nuclear elements during the reconstitution of the female pronucleus in the orthonectids.

The fertilized egg promptly begins to undergo cleavage divisions, leading to the formation of the infusoriform. As more egg cells continue to be freed from the infusorigen the first ones are displaced farther and farther from the infusorigen in the axial cell of the parent rhombogen. Thus there often results from each infusorigen present, a string of embryos with fully formed infusoriforms at the ends. These extend in either direction along the axial cell of the rhombogen.

In infrequent cases the first egg cells ripen and detach from the infusorigen before any sperm are ripe. These either degenerate or produce a compact half-sized embryo that seldom reaches full development.

The infusorigen is not capable of indefinite production of sperm and egg cells but after a certain time appears exhausted. It consists then chiefly of its axial cell, with perhaps a few germ cells still contained in it, a few egg cells attached to it, and numerous sperm scattered about it. Degenerative phenomena and disaggregation as described by Gersch (1938) may be evident during the final stages in the life of the infusorigen. Eventually only its axial nucleus is left lying free in the axial cell of the parent rhombogen, or by now secondary nematogen, where it constitutes the residual nucleus of Whitman (1883).

This account of the infusorigen agrees most closely with those given by Lameere (1916) and by Nouvel (1933, 1947). It differs in all essential points from the account by Gersch (1938) and in several respects from the earlier accounts by van Beneden (1876), Keppin (1892), Whitman (1883), Wheeler (1897), and Hartmann (1904).

THE INFUSORIFORM

(Fig. 10, *a–l*)

From a morphological standpoint the infusoriform is the most complicated stage in the known part of the life cycle of dicyemids. At first glance it appears to bear little resemblance to any of the vermiform stages.

Most earlier writers—van Beneden (1876), Wheeler 1897), Keppin (1892), Hartmann (1906)—believed the infusoriform the male, and some of them—Keppin, Hartmann—even pictured tailed sperm in it. Later authors, Lameere (1918), Nouvel (1933), Gersch (1938) consider it simply a form serving to disseminate the species in a manner analogous to that of a trematode miracidium. The most complete account of the infusoriform has been presented by Nouvel (1948).

To bring out certain details not emphasized in previous accounts and to facilitate discussion of the differences between various accounts of the infusoriform, the morphology of the fully developed infusoriform of *Dicyemennea adscita* will first be presented in detail. The variation between species, the embryology, and the probable role in the life cycle will then be discussed.

MORPHOLOGY OF THE INFUSORIFORM OF *Dicyemennea adscita*

The mature infusoriform is a small bilaterally symmetrical, nearly oval organism about 32μ–36μ long, 26μ–28μ broad at the widest part of the body, and 24μ–25μ deep. It is broadest anteriorly, tapering slightly to a bluntly rounded posterior end.

The anterior end is smooth and chiefly occupied by two large refringent bodies situated in the two anterior-dorsal somatic cells, distending and completely filling them. The posterior part of the body is clothed with long cilia directed backward most of the time.

Near the middle of the body and close to the ventral surface is a group of four cells constituting the contents of the urn. The cytoplasm of these cells stains more densely than that of the other cells of the body. Each of them contains two nuclei plus an enclosed germ cell, similar to an axoblast though much smaller. The cells are arranged to form a sort of hollow cup, open in an antero-ventral direction. The space thus formed communicates directly with the exterior through a small pore in the ventral body wall of the infusoriform. The lateral lips of this pore are slightly raised and can be seen in the living organism when viewed directly from behind or in front.

Enveloping the contents of the urn on all but the open side are two large crescentic capsule cells forming the urn itself. Their nuclei, the largest present in the infusoriform, are located above the cells of the urn contents near their posterior margin, one on either side of the midline. These cells elaborate rounded proteinaceous granules, highly refractile in life, which line their inner margins immediately adjacent to the cells within the urn, forming a sort of jacket or basket-like envelope around them. These also open antero-ventrally toward the ventral pore.

Immediately above and slightly forward from the capsule cells, just below the dorsal ciliated cells are two large flattened cells that have heretofore almost entirely escaped notice. They are shown partly for the first time in the illustrations by McConnaughey (1941) of the infusoriforms of *D. californica* and *D. brevicephala*, but no comment was offered regarding them in that paper. Nouvel (1948) reported their presence, terming them the internal dorsal cells but saying nothing more about them. Their distinctiveness and special characteristics make them of some interest. In ordinary preparations these cells appear as broad, flattened,

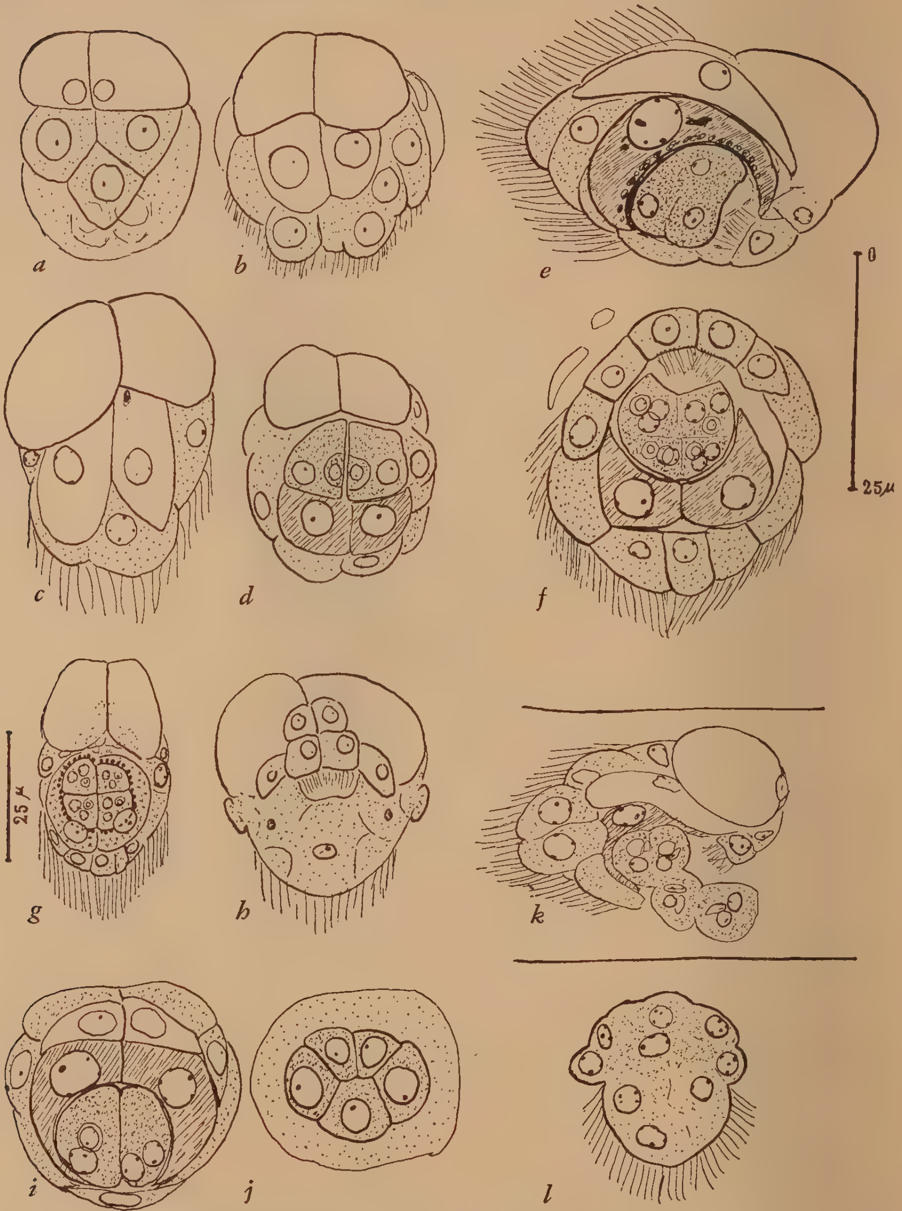

Fig. 10. Morphology of the infusoriform larva. *a. Dicyemennea granularis*, young infusoriform, dorsal surface, showing upper part of the refringent bodies, the nuclei of the cells containing them, and three dorsal ciliated cells. *b.* Optical section of the same individual at slightly lower level showing the two dorsal internal glycogen cells. *c. D. adscita*, optical frontal section of very young infusoriform at level of the dorsal internal glycogen cells. *d. Dicyema acciaccatum*, frontal optical section of very young infusoriform at the level of the urn, showing the invasion of two of the axial-type cells within the urn by the corresponding germ cells. The nucleus of the urn cell on either side has not yet divided to form the two nuclei characteristic germ cells. The nucleus of the urn cell on either side has not yet divided to form the two nuclei characteristic of the mature larva.

nonstaining cells, tilted downward and converging anteriorly between the posterior medial borders of the refringent bodies. Posteriorly they diverge somewhat and extend about three-fourths of the body length. These cells are not stained by ordinary histological stains but appear as clear spaces in the organism. Their nuclei are slightly irregular in shape and degenerate in appearance compared with those of the ciliated epithelial cells.

These two cells were found to store glycogen. Contrary to the results of Nouvel (1929, 1930, 1933), who reported glycogen stored in the ciliated epithelial cells and made no mention of these two special cells in these papers, I find in the species tested, that these two cells alone give a strong positive reaction either with the iodine test for glycogen or with Best's carmine, though traces can sometimes be found in other cells. They are completely negative for the aldehyde test for tryptophane, which gives a positive result for the refractile granules in the capsule cells.

The remaining cells, constituting the majority of the epithelial cells, are divisible into two groups. The ciliated cells cover the dorsal, lateral, posterior, and ventral parts of the body behind the refringent bodies and behind the ventral pore (17 cells). An anterior group of eight smaller lighter staining cells is situated ventrally, beneath the refringent bodies and anterior and lateral to the ventral pore. Four of these, situated immediately in front of the cavity of the urn, are larger than the other four that extend in a posterior dorso-lateral direction from them, two on each side. Two of the first four of these cells form the anterior margin of the cavity of the urn, and from these two cells cilia extend into the cavity of the urn. It is these cilia with their basal granules that were evidently mistaken for sperm by Keppin and Hartmann, as Nouvel (1933) has pointed out.

Lameere considered the eight antero-ventral cells as homologous with the calotte of the vermiform individuals, the cells bearing the refringent bodies as corresponding to the parapolar cells, the rest of the epithelial cells as equivalent to the somatic cells of the trunk, and the urn capsule cells together with the cells within the urn as corresponding to the axial cell and its contained germ cells.

This leaves unaccounted for the two dorsal internal or glycogen cells that were unknown to him and that seem to have no differentiated homolog in the vermiform individuals. Also it seems evident that the two capsular cells of the urn are somatic in character rather than axial. The four cells contained within the urn, each with

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e. Dicyemennea adscita, parasagittal slightly tilted optical section of a mature infusoriform larva showing the glycogen cell, the capsule cell, a part of the urn contents and the cell bearing the internal cilia of the urn cavity of one side. *f. D. abelis,* oblique frontal section of mature infusoriform passing anteriorly below the refringent bodies through the two cells bearing the internal cilia of the urn cavity, and posteriorly dorsally through the contents of the urn, the capsule cells and just below the posterior ends of the glycogen cells. *g. D. californica,* frontal optical section of mature infusoriform at the level of the urn. *h. D. granularis,* mature infusoriform showing disposition of cells on the ventral surface. *i. D. adscita,* transverse optical section of infusoriform. Top to bottom: dorsal ciliated cells; dorsal internal glycogen cells; capsule cells; part of contents of urn; ventral somatic cell. Other somatic ciliated cells lateral in position. *j.* Posterior end of same infusoriform showing in *i,* showing the five caudal cells. *k. Dicyema balamuthi,* parasagittal optical section through an infusoriform in the act of discharging the contents of the urn into the axial cell of the parent rhombogen. *l. D. balamuthi,* abnormal infusoriform of reduced size in which the refringent bodies, the urn and other structures, failed to differentiate. Such larvae are infrequent but when found are usually farthest away from the parent infusorigen in the row of embryos—that is, are the first formed larva. It seems probable that occasionally an egg cell detaches from the infusorigen before the sperm are ripe and produces an abortive embryo.

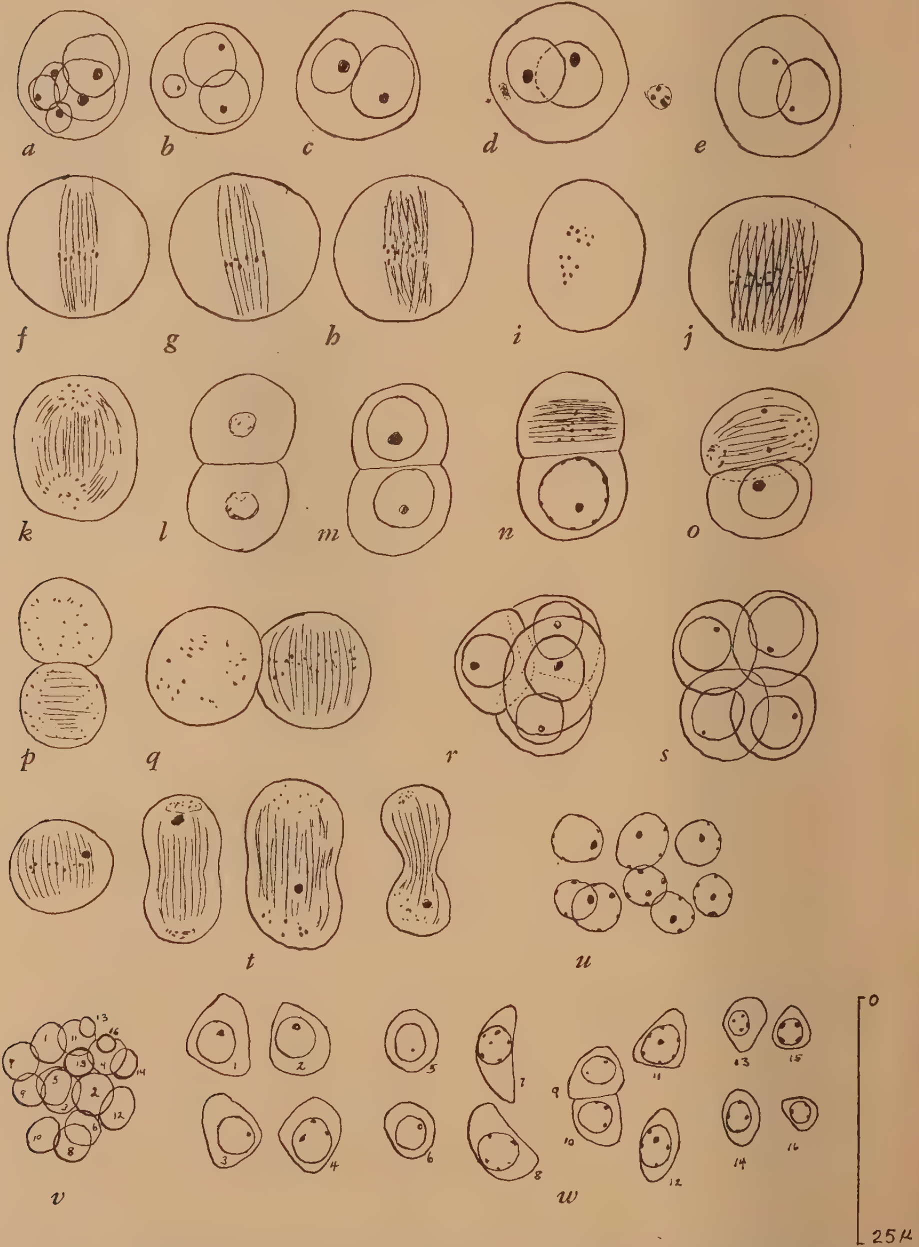

Fig. 11. Embryology of the infusoriform larva. *a, b. Dicyemennea granularis*, fertilized egg cells following elimination of the polar bodies, showing early stages of the reconstitution of the pronuclei. *c, d. D. adscita*, fertilized egg cells showing the male and female pronuclei. In *d* the polar bodies are also shown, one lying beneath, the other to one side of the egg cell. *e. Dicyema apollyoni*, fertilized egg cell with pronuclei. *f, g, h. D. apollyoni*, three views of the same egg cell at metaphase of the first cleavage, showing two spindles each with apparently seven chromosomes: *f.* High focal level. *g.* Lower focal level without change in orientation. *h.* Both views combined. *i.* Polar view of similar egg cell at metaphase of first cleavage. One of the chromosome groups

its two nuclei and inclosed germ cell, apparently do correspond to axial cells. The capsule cells might perhaps be considered modified uropolar cells.

Lameere's contention that the structure of the infusoriform represents a highly modified but recognizable vermiform individual seems to have good basis in fact. In any event it clarifies the discussion of the infusoriform and reduces it to a grade of organization coördinate with that of other stages in the life cycle.

Variation between Species

The infusoriforms of different species of dicyemids are remarkably uniform in structure. There is some variation in the size attained. Some are almost evenly rounded, others taper to a conical point behind. The cell number may vary slightly but this has not been established with certainty. A few species have only one nucleus in addition to the germ cell in each cell within the urn. Some species apparently void the contents of the urn more readily than others. The aspect of the nuclei, their size, the clumping of chromatin, staining characteristics of the cytoplasm, and the size of the refringent bodies also differ in some degree between various species.

Embryology of the Infusoriform

The male and female pronuclei of the fertilized egg do not fuse before the first cleavage but each breaks down and resolves itself into a group of chromosomes that become arranged on separate spindles. Sometimes it is possible to distinguish readily the two groups of chromosomes at the metaphase and to observe that the spindles are separate or even oriented in a slightly different direction (fig. 11, *f–j*).

The first cleavage results in two cells of equal size with no readily distinguishable differences between them.

In the second cleavage the two cells divide in an orientation at right angles to each other so that often one of the blastomeres is observed from an equatorial, the other from a polar point of view. The four resulting cells are of equal size and not yet differentiated into recognizable classes. In some cases at least it is seen that during the telophase one or two larger pieces of chromatin lag behind on the spindle of one of the pairs of blastomeres, but not the other pair. These are eliminated as small vesicles containing chromatin, similar to those eliminated by young vermiform embryos.

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appears to have seven, the other eight, chromosomes, though the eighth is so minute as to be uncertain. *j. Dicyemennea brevicephala,* metaphase of first cleavage showing two spindles in slightly different orientation. *k, l, m. D. adscita,* final stages of first cleavage and formation of two-celled embryo. *n. Dicyema apollyoni,* two-celled embryo, one of the cells entering upon the second cleavage division. *o. Dicyemennea adscita,* two-celled embryo, one cell in late anaphase of second cleavage. Two pieces of residual chromatin can be seen lagging behind on the spindle. *p. D. granularis,* two-celled embryo, both cells undergoing second cleavage division. *q. D. californica,* similar stage. *r, s. D. adscita,* four-celled embryos. *t. D. californica,* selected blastomeres from embryos during the second or third cleavage showing residual chromatin that lags behind on the spindle and passes to one of the resulting cells, later eliminated from the developing embryo. *u. D. adscita,* nuclei of an eight-celled embryo showing differentiation into four large and four slightly smaller cells. *v. D. adscita,* nuclei of a sixteen-celled embryo. *w.* The individual cells of the same embryo drawn separately to show cellular differentiation attained at the sixteen-cell stage. The four small cells (13–16) are the future germ cells each of which later invades one of the four larger cells (9–12) making up the contents of the urn. The two crescentic cells (7, 8) are the capsule cells of the urn. The other cells are not definitely identifiable at this stage. It appears that two of them (? 5, 6) may be the two dorsal internal glycogen cells. The remainder probably represent the ordinary somatic cells.

The third cleavage results in an eight-celled morula of which four cells are just slightly smaller than the other four.

In the sixteen-cell stage (fig. 11, *v–w*) we find the first obvious and clear-cut differentiation. Here four small cells—the future germ cells—have been cut off internally from four slightly larger ones which they later invade, and which are the future contents of the urn. There are also at this time visible differences among the somatic cells. Two larger crescentic ones represent the capsule cells of the urn. Another pair probably are the two glycogen cells.

The four germ cells undergo no further division. The four cells representing the contents of the urn remain quiescent until they have been invaded by their respective germ cells. Then each undergoes one mitotic nuclear division not followed by a cytoplasmic division, which results in the definitive condition found in the fully formed infusoriform. A few species are reported to have only one nucleus in addition to the germ cell. In these this second division has evidently been repressed.

Meantime the other somatic cells have continued to divide, though not all at the same rate. By the time the embryo has attained the thirty-two-nucleus (28-cell) stage the anterior ventral group of cells in front of the urn and below the refringent bodies are set apart from the other somatic cells and the two refringent bodies are beginning to form. They are first evident as tiny pinhead-size clear vesicles in the cytoplasm of the anterior dorsal pair of somatic cells. They enlarge progressively till they distend the cell, occupying its whole volume and pushing the nucleus up against the cell wall.

Around the refringent bodies, especially on their ventral, medial, and posterior surfaces, are deposited small globules of another refractile substance, giving the surface a pebbled appearance similar to that of the sheath of proteinaceous granules surrounding the contents of the urn on all but one side. These granules may be the source of the secretion liberated by the infusoriform just before its escape from the parent rhombogen. They can be seen most easily in the living infusoriform.

Nouvel (1947) described for *Dicyema schulzianum* and *Dicyemennea lameerei*, and implied for other species, a very unusual course of events in the fertilization of the egg cells.

According to his account there is only one division resulting in polar body expulsion. This takes place after the penetration of the egg cell by the sperm. The chromosome number in the egg nucleus is still diploid. This is followed by the expulsion of the sperm. The egg nucleus may then undergo a division without giving off a polar body. The two nuclei thus formed reunite, forming a single diploid nucleus entirely derived from the original egg nucleus. The cell then proceeds to undergo cleavage and to form the infusoriform larva.

This is at variance with all earlier accounts, though there had been no agreement among former writers as to what takes place at this time. It is also contrary to my own observations.

Polar body emission is correctly described by Nouvel, but this is the second polar body that is formed. Formation of the first one, which happens while the egg cell is still in contact with, or very close to the infusorigen, is rapid and difficult to detect.

I have found no evidence that the sperm is expelled from the egg before the first cleavage. It is possible that the small sperm-like body found adherent to early embryonic infusoriforms is the product of chromatin elimination similar to that taking place in young vermiform embryos. In the case of the infusoriform the eliminated chromatin tends to adhere more closely to the developing embryo than in the vermiform larva. Sometimes an additional sperm cell is found attached to the surface of a developing embryo. This could well account for such occasional appearances as shown in figure 51 D of Nouvel (1947).

Escape and Behavior of the Infusoriform

When fully developed, the infusoriform becomes active while still inside the axial cell of the parent rhombogen. Its activity consists primarily in turning over and over in the same place, though it may sometimes push its way for some distance along the axial cell. Before its escape the infusoriform liberates a secretion from around the refringent bodies that causes the formation of a large vacuole around it. This vacuole grows progressively till the body of the rhombogen is distended at this point and the epithelium very thin and stretched out. The infusoriform acts as though partly paralyzed. With its cilia held rigidly in a reversed direction, it is gradually squeezed out backward, together with the contents of the vacuole, through the side of the rhombogen which immediately closes up, leaving no scar or any visible trace of the point of rupture. The liberated infusoriform sometimes swims away almost at once, sometimes remains nearly motionless with its cilia held rigidly in a reversed direction for one or two minutes before swimming off.

Once active, the infusoriforms are able to swim very rapidly. They usually go at once to the bottom of any vessel in which they are put and swim about over the bottom. When uninterrupted they may go an inch or more in a straight line, rotating on their long axes as they swim. If an infected cephalopod containing rhombogens is kept in a jar of sea water for several hours a large number of infusoriforms can usually be recovered by placing the water in a large separatory funnel and drawing them off at the bottom a few minutes later.

When placed in a small vessel of sea water or diluted octopus urine under a dissecting microscope, the living infusoriforms showed no apparent interest in other stages of dicyemids introduced into the water with them, no interest in newly hatched young octopus or squid, nor in any of the other animals so far tested, though their small size renders it difficult to tell in most cases. Surface scrapings or extracts of various intertidal animals, especially bottom forms, introduced among active infusoriforms in the ends of capillary tubes brought no noticeable response. After twelve hours or more in sea water some of them will usually be found to have voided the contents of the urn or to be undergoing general disaggregation. As a rule they do not live more than three or four days in small aquaria with aerated water. Specimens fixed after several hours of swimming about in sea water showed no significant changes in their structure, contrary to statements by Gersch and others.

When a number of living infusoriforms are observed on a slide under the microscope it is not unusual to see one of them swim about rapidly in an agitated manner, suddenly pause or move in a small circle and discharge from the posterior end a large number of sperm-like bodies. These continue to squirm about independently for a time. They correspond closely to the sperm figured by Keppin (1892) and Hartmann (1907). The infusoriform may swim on, and in a short period, discharge two or three groups of these sperm-like bodies.

This observation at first seemed to support the contention that the infusoriform is the male, but careful study of the process showed that it is actually only the first step in the disaggregation of the individual. The sperm-like bodies are cilia with their basal granules, which come off in considerable numbers and sometimes leave the infusoriform almost bare or with irregular patches of cilia. The infusoriform itself usually undergoes general disaggregation within ten to fifteen minutes after it begins to lose cilia. The process occurs most frequently when the preparation has begun to lose water by evaporation so that the concentration of salts is increased.

THE SECONDARY NEMATOGEN

Occasionally a cephalopod is found in which some of the dicyemids show the secondary characteristics of rhombogens (accessory nuclei in the somatic and axial cells) but are giving rise to a generation of vermiform larvae. Often there are even one or more mature infusorigens present, with egg cells and infusoriform embryos to an advanced morula stage. These morulae then appear to disaggregate instead of completing their development. Usually a large number of axoblasts are present.

There has been little agreement about the phenomena leading to the resumption of nematogenic activity by rhombogens, and Gersch (1938) has even denied that it occurs at all.

That it does sometimes happen there can be no doubt. The writer has found cases that allow of no other interpretation, that is, individuals with advanced infusorigens and infusoriform embryos together with young vermiform embryos in the earliest stages of development. Several questions, however, need further clarification: 1. What is the source of the axoblasts from which the new generation of vermiform larvae arises? 2. Are these vermiform larvae essentially different from those produced by primary nematogens? 3. Is the phenomenon a regular and necessary part in the life cycle or something that happens under special conditions and perhaps only in certain species?

Whitman (1893) and Hartmann (1906) believed that the last germ cells produced by the infusorigen, instead of developing into egg cells and producing infusoriforms, simply divide to form axoblasts or develop directly into vermiform embryos. It was believed that these embryos were capable of tolerating sea water and migrating to other cephalopods where they start new infections and await fertilization by males (infusoriforms) which likewise were thought to migrate from one cephalopod to another.

Benham (1901), in Lankester's *Treatise on Zoology,* stated that the peripheral cells of the infusorigen form egg cells that become infusoriforms [after which] the germ cells within the axial cell of the infusorigen are liberated and give rise to vermiform larvae. This is probably a misreading of the literature by Benham, as he is not known to have studied the dicyemids directly.

Lameere (1916) and Nouvel (1933) believed that the cells of the developing infusoriform, upon its disaggregation, become axoblasts producing new vermiform larvae, which thus arise by a peculiar sort of polyembryony—the cells of one sort of highly specialized individual reverting, midway in its development, to the condition of primitive germ cells and giving rise to individuals of a very different sort. According to them the vermiform larvae so engendered do not migrate from one cephalopod to another but simply continue the infection in the same host in the same manner as the ordinary vermiform larvae. This view was also adopted in my brief review of the life cycle (1938).

After a restudy of the question I have arrived at a different interpretation which, however, cannot be said to be conclusively established. It is frequently found that in active rhombogens a few ordinary axoblasts still persist, apparently in good condition. It is thought that under certain conditions these are able to resume their activity and again begin producing more axoblasts and vermiform larvae in the usual manner. This would leave the infusorigen and its products out of the picture as far as the production of vermiform larvae is concerned.

During the period of transition from nematogen to rhombogen it is sometimes noticeable that the last vermiform larvae appear stunted and poorly developed. It would seem that there is a competition between the products of the two modes of reproduction for the available nutritive substances dissolved in the axial cell, that the production of infusoriforms is the more vigorous and suppresses the activity of the axoblasts through starvation and possibly also by some direct influence. At the time of exhaustion of the infusorigens, when their activity is reduced or stopped, it is thought that the situation may be reversed, and that any axoblasts that have survived and persisted through the period of rhombogenic reproduction may be able to resume their activity and produce one or more generations of vermiform larvae before the death of the old rhombogen. The resumption of the nematogenic mode of reproduction is viewed, not as a constant and invariable part of the life cycle but as a more or less accidental consequence of the persistence of some axoblasts in good condition through the rhombogen period in some of the individuals.

RÉSUMÉ OF THE LIFE CYCLE

The known part of the life cycle as interpreted in this paper is summarized in figure 12. A single arrow represents a new generation arising from germ cells within the preceding. A double arrow indicates merely the transformation of an individual from one phase to another. Parenthesis indicates that the form inclosed does not leave the axial cell of the individual in which it arose.

GENERAL CONSIDERATIONS

Specialization Within the Group

The dicyemids show a number of peculiarities that can be interpreted as possibly pointing out the general directions in which specialization has proceeded within the group. It will be convenient to think of these in two categories: (a) primitive or generalized characteristics that appear during the embryological development of some or all species and that are more clearly retained in some than in others;

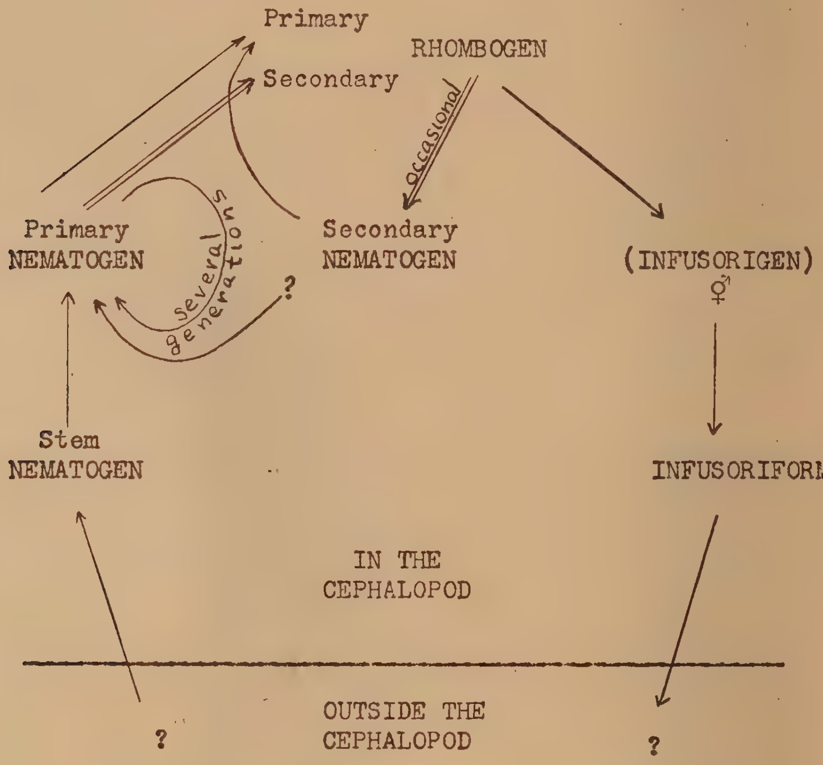
Primary
Secondary
RHOMBOGEN
occasional
Primary
NEMATOGEN
several generations
?
Secondary
NEMATOGEN
(INFUSORIGEN)
⚥
Stem
NEMATOGEN
INFUSORIFORM
IN THE
CEPHALOPOD
OUTSIDE THE
CEPHALOPOD
?
?

Fig. 12. Diagram of the life cycle as interpreted in this paper.

(b) terminal specializations, specialized conditions, or adaptations of particular species or groups of species.

These can be arranged in related pairs showing general trends from more generalized to more specialized conditions as follows:

GENERALIZED	SPECIALIZED
1. large, variable number of somatic cells.	reduced number of somatic cells, tendency to constant number.
2. medium to large size, prolific formation of embryos.	very small size, few embryos.
3. conical orthotropal calotte.	discoid or plagiotropal calotte.
4. axial cell not penetrating the calotte to the propolar cells.	axial cell penetrates forward to the propolar cells, often inflated and in extreme cases (heterocyemid condition) branching into inflated cells of the calotte.
5. second axial cell present as small abortive cell in vermiform larvae.	no second axial cell present in the vermiform larvae.
6. axial and paranuclei maintain their integrity.	additional free nuclei frequently present besides the axial and paranuclei.

7. axial cell nucleus of inclosed vermiform larvae located between the first two axoblasts when larva attains full development.	axial cell nucleus of inclosed vermiform larvae anterior to the first two axoblasts in developed larvae. Further multiplication of axoblasts may occur in larva before its escape from parent nematogen.
8. caudal somatic cells verruciform, other verruciform cells frequently present.	caudal cells not verruciform, some species without any verruciform cells.
9. infusoriform with two nuclei and one germ cell in each cell in the urn.	infusoriform with one nucleus and one germ cell in each cell in the urn.

If we accept the foregoing criteria of what constitute generalized and specialized conditions within the group it becomes apparent that the genus *Dicyemennea* rather than *Dicyema* is the more generalized and primitive.

Within each genus there are some species that seem to represent best the generalized generic type or model characteristics, and various species or small groups of species showing departures from this in certain directions.

Thus within genus *Dicyemennea, D. californica, D. abelis, D. acscita,* and *D. granularis* seem to represent the generalized condition very well. *D. lameerei* and *D. abasi* show much reduction in size, loss of verruciform cells, and, in *D. lameerei,* a forward extension of the axial cell to the propolars. *D. brevicephala* and *D. abbreviata* show greater cell constancy, increasing flattening of the calotte, increasing disproportion in size between the pro- and metapolar cells, and increasing differentiation of the cephalic swelling leading to the condition in the heterocyemid *Conocyema adminicula. D. eledones* and *D. gracile* show unusually large size together with loss of verruciform cells and, in *D. gracile,* of the larval second axial cell. In them the axial cell extends forward to the propolars, being broadly rounded or even somewhat inflated within the calotte.

Genus *Dicyema* as a whole is characterized by one less metapolar cell with no second axial cell rudiment in the larvae. There is a tendency for the axial cell to extend forward into the calotte, swelling somewhat at the anterior end. Likewise it has a tendency toward irregularities in the free nuclei within the axial cell, caused by amitotic divisions of the axial cell nucleus or of some of the paranuclei, together with formation of other free nuclei or nucleus-like bodies from some of the germ cells without direct relation to the formation of infusorigens.

Typical species—*D. microcephalum, D. clausianum, D. moschatum, D. macrocephalum, D. balamuthi, D. apollyoni, D. misakiense,* and *D. typus* are similar but with lower cell count, no verruciform cells, and slightly smaller average size. *D. orientale* and *D. schulzianum* show a tendency toward a flattening and telescoping of the cells of the calotte, reminding one of the condition in *Dicyemennea brevicephala.* This is even more pronounced in *Dicyema truncatum,* which in addition shows a rotation of the position of the metapolar cells relative to that of the propolars. In this genus the three species in which the axial cell ends anteriorly at the posterior end of the metapolar cells—*D. monodi, D. acciaccatum,* and *D. acheroni*—are all small, without verruciform cells, and in general seem specialized and atypical rather than primitive and generalized. It seems possible that they may have arisen separately from the other species of the genus.

D. sullivani is similar to the more typical members of the genus in size and cell number but does not exhibit the foreward extension of the axial cell to the propolars shown by most of them.

AXIAL CELL

It may be useful to bring together in one place a summary of observations and conjectures on the axial cell, its relation to the germ cells and to the reproductive cells of the orthonectids.

In the most generalized orthonectids the egg cells of the female form a compact mass filling the body and surrounded by a single layer of ciliated somatic cells. The sperm are developed in a discrete testis (fig. 13, *a*).

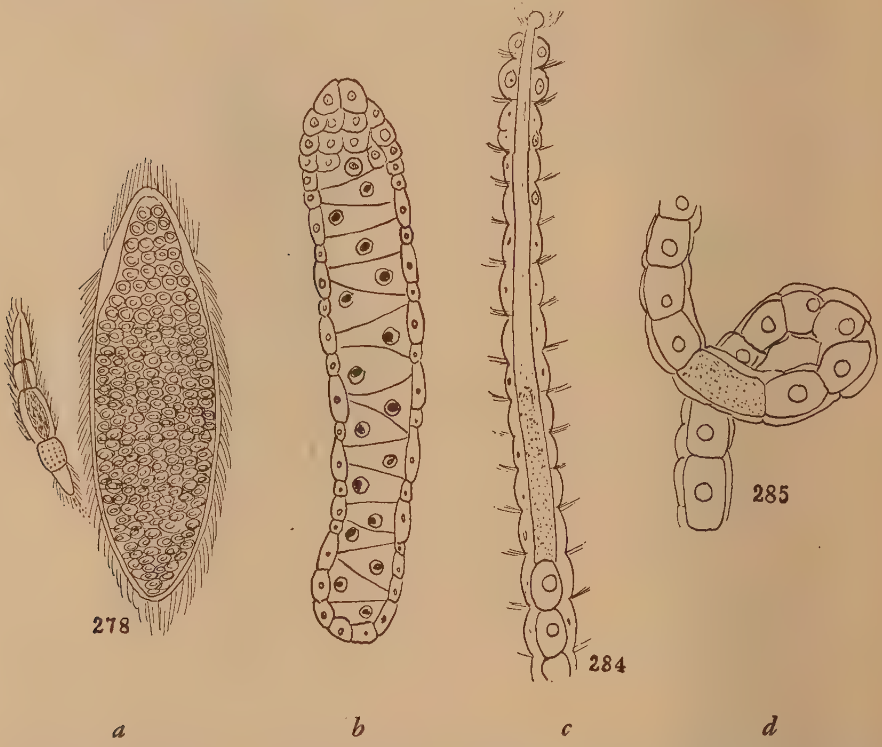

Fig. 13. Orthonectids. *a.* Typical orthonectid, *Rhopalura ophiocomae*, male discharging sperm near the genital pore of the female. From Lameere after Caullery and Lavallee. *b. R. metschnikovi*, female, germ cells oriented in a double row. From Hartmann after Caullery and Mesnil. *c. Stoechartrum giardia*, anterior end. *d. S. giardia*, part of trunk showing egg cells in single linear series, one to each apparent segment. One of the segments has developed as a testis. From Caullery and Mesnil.

In some species the ova are aligned in one or two longitudinal rows (fig. 13, *b*).

Stoechartrum has a long filiform body with an appearance of segmentation, each division of the body containing one ovum. The organism is hermaphroditic. The segments constituting testes produce many spermatozoa (fig. 13, *c–d*).

In the stem nematogens of dicyemids there are three (two in one species) large axial cells in linear series. The young larvae show an additional cordon of several aborted axial cells anterior to the definitive ones.

In embryonic vermiform larvae of most *Dicyemennea* there are two axial cells, one abortive. The first germ cell or axoblast is formed by a complete cell division of the large central cell of the young embryo so that there is formed a row of three internal cells surrounded by the somatic cells. The anterior cell, representing an abortive axial cell, degenerates; the large central cell becomes the definitive axial cell; the posterior cell constitutes the first axoblast and invades the axial cell.

In larval *Dicyema* the small abortive second axial cell is not usually formed; only the definitive axial cell and the first axoblast are found in the young larvae.

The early embryology of the infusorigen differs from that of a vermiform larva chiefly in the precocious development of the axial elements. Instead of remaining quiescent until somatic cells have largely surrounded the central cell, the differentiation of axial elements starts first and continues simultaneously with the early differentiation of the peripheral cells. The first distinctive act is the elimination of a small cell that becomes the paranucleus. This is here interpreted as equivalent to the first division of the central cell in larval *Dicyemennea* with the formation of an abortive second axial cell. In this case, the eliminated cell, not being inclosed in a developing embryo but lying free in the axial cell of the parent rhombogen, develops into a large nucleus-like body—the paranucleus of Whitman. The formation of the first internal germ cell proceeds as in vermiform larvae but much earlier, before the axial cell is surrounded by peripheral cells. The later fate of the peripheral and internal cells differs altogether from that of the corresponding cells in vermiform embryos.

In the infusoriform embryos the four axial, or urn, cells and four germ cells are set apart at the sixteen-cell stage. Each germ cell later invades the corresponding urn cell. In most species there is a single additional mitosis of each urn cell nucleus not followed by cytoplasmic division so that each of the four cells consists of a binucleated cell enclosing one germ cell. These four cells constitute the contents of the urn of the infusoriform.

Thus in all known stages of the dicyemids each axial cell and the corresponding first inclosed germ cell are at first coördinate cells derived from a mitotic division of a single large reproductive cell. Further, in those forms and stages in which more than one axial cell is represented, the additional axial cells appear to be derived by early division of a single original cell representing all the reproductive and axial elements in the embryo. This is certainly true in the case of larval primary nematogens of *Dicyemennea* and presumably true for larval stem nematogens.

It seems then that Lameere's concept that the axial cell is a primitive germ cell that has lost its reproductive capacity and developed into a large follicular cell for the protection and nourishment of the other germ cells and embryos developed from them, is correct.

The evidence indicates that the ancestral form for the dicyemids was probably a ciliated sexual vermiform organism with a linear series of inclosed reproductive cells. Among the orthonectids *Stoechartrum* fits this formula rather well and exhibits a grade of organization indicating a probably close relationship between this genus and the forms from which the dicyemids were derived.

The principal innovations in dicyemid organization are the inclosure of the active reproductive cells in one or a few large follicular cells, the axial cells, and the curious degradation of the sexual generation to a mere group of reproductive cells that never leaves the axial cell of the form giving rise to it.

A definitive conclusion regarding the phylogenetic relationships of the dicyemids must, however, await an elucidation of the unknown part of the life cycle between the infusoriform and the stem nematogen.

CAUSE OF THE CHANGE OF PHASE

The factors that bring about the change from the nematogen to the rhombogen phase are not clear. That the change occurs in most of the individuals present in a cephalopod at about the same time, and that young individuals liberated during this time or afterward apparently develop directly into rhombogens without previously functioning as nematogens, indicate that the change of phase is probably induced by some environmental agency affecting the whole population rather than being simply a maturing of the individual parasites.

The change does not appear seasonal in character, as populations of rhombogens are found in mature octopuses at all times of the year, whereas young octopuses taken at the same time harbor nematogens.

The fact that the change generally occurs at about the time the host reaches sexual maturity has suggested to several investigators that humoral changes in the host, incident to the attainment of sexual maturity, are responsible for the change in the parasites. This is a very plausible theory since in various other groups, humoral changes of animals have been shown to exert far-reaching effects upon their parasites, but as yet there is no experimental evidence in this instance.

The fact that occasional nematogens can usually be found by careful search even in populations predominantly rhombogen, and that certain clusters of individuals may be composed chiefly of nematogens whereas others in the same cephalopod are predominantly rhombogen show that, whatever the cause of the change, it is not uniformly and simultaneously operative over the entire population. This suggests that perhaps the parasites themselves may be at least partly responsible for the changes; that the great crowding of the parasite population with consequent alteration of conditions within the host kidney or urine, perhaps the liberation of metabolic products or hormones or the depletion of available nutrients by the parasites, induces the change. The fact that the change of phase is accompanied by numerous degenerative alterations, as amitotic division of the somatic nuclei and extensive degeneration and digestion of the axoblasts, lends some support to this hypothesis. Uneven population and crowding of the various kidney lobules might account for irregularity of the change of phase between different clusters of parasites in the same host.

SUMMARY

The known part of the life cycle of the dicyemids is essentially that presented by Lameere (1916, 1918, 1919).

The possible derivation of the dicyemids from *Stoechartrum*-like orthonectiform ancestors is discussed. Within the dicyemid group the genus *Dicyemennea* rather than *Dicyema* appears to contain the more primitive generalized members. The heterocyemids are regarded as extreme modifications of the dicyemid form, possibly polyphyletic in origin.

The existence of stem nematogens and of secondary nematogens for some species has been confirmed. A simpler explanation of the origin of the axoblasts giving rise to vermiform larvae in secondary nematogens is suggested.

The origin and fate of the small degenerate cell just anterior to the axial cell in larval *Dicyemennea* is traced. It is interpreted as a rudimentary second axial cell and its possible phylogenetic significance discussed.

The chromatin granules eliminated by young vermiform and infusoriform embryos are interpreted in the light of the theory recently offered by Goldschmidt and Lin (1947) concerning chromatin diminution in cell-constant animals. It is shown that this elimination occurs only from the vermiform and infusoriform embryos, which develop into cell-constant stages, but not from embryonic infusorigens in which all the cells become reproductive cells.

The relationship of the paranuclei to the infusorigens is confirmed. The paranucleus itself is regarded as an aborted second axial cell of the infusorigen, morphologically equivalent to that formed by larval *Dicyemennea.*

The hermaphroditic character of the infusorigen is confirmed. The formation of sperm and egg cells by the infusorigen is confirmed. Chromosome reduction is demonstrated for one species and indicated though not proved for others. Fertilization and restoration of the diploid chromosome number is demonstrated. The sperm plays a normal role in the fertilization of the egg cell.

The morphology of the infusoriform is examined in greater detail than heretofore. It is considered a swarming form serving to disseminate the parasite, presumably to another host species, somewhat in the manner of a miracidium. The two dorsal internal cells are shown to store glycogen. A simplified method of obtaining living infusoriforms in large numbers for infection experiments was devised. All such experiments to date have given negative results.

Both male and female octopuses were found to shed infusoriforms at all times of the year without regard to the breeding season. They were not found to shed vermiform larvae.

The relationship of the Mesozoa as a whole to other groups of animals is still obscure, though it seems probable that they were derived from higher metazoa rather than forming an intermediate link between these and the protozoa, as several writers have already maintained.

The flatworms, the echiurans, and the coelenterates have been suggested by various authors as probable ancestors of the Mesozoa. Perhaps the most acceptable opinion is that expressed by Stunkard (1937) who regards them as degenerate or highly specialized flatworms, derived, not from any existing group of the Turbellaria, but from a remote ancestor of all present flatworms, probably before the origin of the digenetic trematodes or cestodes.

Hyman (1940) has suggested that their structure may indicate that one of the earliest steps in metazoan organization was the relegation of the reproductive cells to the interior, rather than the formation of a hollow gastrula.

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Reprinted from Biological Bulletin, Vol. 101, No. 1, 84–94, August, 1951
Printed in U. S. A.

THE UPTAKE OF VANADIUM BY TUNICATES

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THE UPTAKE OF VANADIUM BY TUNICATES[1]

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The ability of certain ascidians to concentrate vanadium was first reported in 1911 by Henze (1911), who found this element in the blood of four species. Since then more than a score of papers have extended these investigations.[2] The scope of the above work has included the analyses of various species of ascidians to determine the presence or absence of vanadium, and experiments to indicate any possible physiological function of the vanadium.

The first phase of these studies culminated in the work of Webb (1939) who was able to correlate the presence of vanadium in ascidians with certain evolutionary traits of the class. Webb concluded that vanadium is concentrated by the primitive species and that this enrichment ability has been lost in the later, more specialized, branches of the class.

Webb also systematically studied the physiological role of vanadium. He demonstrated that the green chromogen containing the vanadium in some species is located in a singular type of blood cell which he called the "vanadocyte." Later, however, in histological investigations on certain Japanese ascidians, Ohuye (1936) described what may be the same type of green cells in these animals which, according to the analyses of Kobayashi (1948), contained no vanadium. Webb found no physiological function for the vanadium, although previously it had been assumed to be associated with a blood respiratory pigment. He also postulated that the vanadium was incorporated in a rectilinear chain of pyrrole rings rather than in a protein or porphyrin complex.

The reported distribution of the vanadium within ascidians is somewhat contradictory. Webb suggested that all of the vanadium is located in the blood, whereas the experiments of Kobayashi and of Bertrand localized the majority of the vanadium in other parts of the animal. In *Ascidia mentula* Bertrand found ⅔ of the vanadium in the tunic, yet Kobayashi was able to establish only traces of vanadium existing in the outer covering of Japanese ascidians.

The dynamics of the concentration of vanadium from sea water by these marine animals has received scant attention. Bertrand describes the situation as a complete mystery and states that the vanadium could come neither from sea water, which is very poor in vanadium, nor from vanadium-impoverished marine muds in the vicinity of the ascidians. He invites research on plankton as a potential source of vanadium. Rankama and Sahama (1950) suggest, however, that the vanadium is collected by ascidians directly from sea water.

Thus, from a biogeochemical standpoint it seemed desirable to investigate the more intimate details of the concentration of vanadium by marine organisms. The present investigation was undertaken in order to attempt to follow the transfer of vanadium from the sea into the various parts of the body of ascidians. A knowledge of the mode of uptake and its histological distribution might shed light upon a possible role played by the vanadium.

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[1] Contributions of the Scripps Institution of Oceanography, New Series No. 528.

[2] A comprehensive survey of the biogeochemistry of vanadium has been prepared by D. Bertrand (1950).

To lay the groundwork for these investigations, chemical analyses of dissected portions of some local ascidians were made. This work was intended to establish more definitely the sites of vanadium concentration. A limited number of analyses were made on the total vanadium content of some local species for inclusion in Webb's phylogenetic table.

Cyclotron-produced radioactive vanadium, free from any inert vanadium carrier, was utilized to follow the assimilation of the element. Radioautographs were made to confirm the results of the chemical analyses and also to point out any smaller loci of vanadium concentration not detected by the less sensitive chemical method.

The authors wish to express their appreciation for the aid given by Dr. Denis L. Fox, Professor of Biochemistry at the Scripps Institution of Oceanography, for his help in the completion of this problem.

Chemical Analytical Techniques

Specimens of *Ciona intestinalis* were collected from floats in Mission Bay, San Diego, California. The *Ascidia ceratodes* specimens were obtained from dredgings in Tamales Bay, Marin County, north of San Francisco, California.

Table I

Vanadium content of Ciona intestinalis

Specimen A			Specimen B		
Sample	Dry Wt.	Vanadium	Sample	Dry Wt.	Vanadium
	grams	γ		*grams*	γ
Tunic	0.1629	0.0	Tunic	0.3317	0.0
Mantle	—	—	Mantle	0.0709	0.0
Ovary	0.0330	2.5	Ovary	0.0241	0.0
Heart	0.0084	0.0	Heart	0.0113	0.0
Incurrent Syphon	—	—	Incurrent Syphon	0.0368	4.0
Excurrent Syphon	—	—	Excurrent Syphon	0.0228	0.0
Esophagus	—	—	Esophagus	0.0014	0.0
Branchial Basket	—	—	Branchial Basket	0.0241	0.0
Gut			Gut		
Anterior Half	0.0517	19.7	Anterior Half	0.1116	21.9
Posterior Half	0.1375	8.9	Posterior Half	0.1252	37.8
Stomach	0.0543	18.8	Stomach	0.0586	9.2
Rest of Specimen and Rinse	0.2299	27.0	Rest of Specimen and Rinse	—	—
Rinse		—	Rinse	0.2955	19.6
Total	0.6777	76.9	Total	1.1140	92.5
Date Ciona Obtained	24 July 1950		Date Ciona Obtained	20 April 1950	
Wet Weight	19.0 grams		Wet Weight	19.0 grams	
Length	8.0 cm		Length	6.5 cm	

TABLE II

Total vanadium contents of some ascidians

Ascidian	Parts Vanadium Per Million
Styella montereyensis	0
Styella bonharti	0
Euherdmania claviformis	475
Ciona intestinalis	100

The specimens were cleaned of adhering dirt and sessile organisms by the light application of a tooth brush. After dissection the individual samples were placed in weighed 50 ml. Pyrex centrifuge tubes. The tube and contents were dried overnight at 110° C., cooled in a desiccator, and weighed to determine the "dry weight" of the sample.

The organic matter was removed by a wet digestion as follows: to the sample-containing tube, 3.0 ml. of a solution of one part concentrated sulfuric acid to three parts of 60 per cent perchloric acid were added. The tube was heated gently with a micro-burner until the sample was nearly completely digested. Stronger heat was then applied to facilitate the complete removal of the perchloric acid. The sulfuric acid residue was diluted to 40 ml. with distilled water, and any remaining solids (usually diatom frustules) were removed by centrifugation.

The vanadium in the clear solution was determined by a spectrophotometric analysis of the vanadium 8-hydroxyquinolate in iso-amyl alcohol according to the method of Bach and Trelles (1941). The samples were read at 480 mμ in 50 mm. cells on a Beckman Model DU Spectrophotometer.

The results of two typical analyses of *Ciona intestinalis* are summarized in Table I. The vanadium concentrations for other ascidians collected during the course of these investigations are listed in Table II.

Relatively high concentrations of vanadium occur in the gut. The gut tube was arbitrarily dissected into four serial lengths. It was found that the highest vanadium concentrations per unit weight were associated with that part of the gut nearest the stomach, and with the segment adjoining the anus (Table III). Vanadium was normally detected in the stomach by these chemical analyses.

Vanadium was also found in fecal pellets in concentrations ranging from 0 to 800 parts per million by weight. Fecal pellets discharged by the animal during its relaxation before dissection, or dislodged during the dissection, may account for the high vanadium content of the rinse water as noted in Table I.

TABLE III

Concentration of vanadium in gut sections of Specimen B

Section	Length	Dry Weight	Vanadium
1 Next to Stomach	10 mm.	0.0601 gr.	19.3γ
2 Next segment	10 mm.	0.0515 gr.	2.6γ
3 Next segment	10 mm.	0.0601 gr.	11.8γ
4 Next to Anus	10 mm.	0.0651 gr.	26.0γ

FEEDING EXPERIMENTS UTILIZING RADIOACTIVE VANADIUM

V^{48}, a positron and gamma ray-emitting nuclide with a half-life of sixteen days, was prepared by the deuteron bombardment of a titanium target according to the reactions $Ti^{47}(d,n)V^{48}$ and $Ti^{48}(d,2n)V^{48}$. The bombardments were made at the 60-inch Crocker Cyclotron in Berkeley, California, with 20 Mev deuterons for one hour with a total irradiation of 7 micro-ampere hours. The titanium target was composed of one gram of the C.P. metal powder supported on a copper plate covered with a 0.25 mil tantalum foil.

The sub-micro amounts of V^{48} were extracted from the titanium powder to give a carrier-free saline solution of radioactive vanadate, following the method of Haymond, Maxwell, Garrison and Hamilton (1950). The nuclide V^{48} was identified by its half life and by aluminum absorption curves to establish the 0.7 Mev positron reported by Peacock and Deutsch (1946).

Individual ascidians were then placed in aerated Pyrex containers which held two liters of sea water. These aquaria were kept in a cold room maintained at a temperature of 12° ± 2° C.

The sea water was normally filtered before use. In preliminary experiments it was found that the radioactive vanadium was adsorbed on particulate matter in non-filtered sea water and was thus removed from solution. The water was filtered through either Whatman No. 42 paper or a diatomaceous earth column. The radioactive vanadium was added after filtration.

The activity of the solution was assayed daily by evaporating under an infrared lamp a one-ml. aliquot of the sea water in a steel cup. The activity of the sample was counted under an end-window tube with a window thickness of 1.4 mg./cm².

A control aquarium was set up without an ascidian to determine whether there was adsorption of the radioactive vanadium on the walls of the container. No measureable adsorption was found to take place.

The initial counting rate of the radioactive solution was about 250 counts per minute per ml. of solution. The counter geometry was estimated at 5 per cent for 0.7 Mev positrons from measurements with a calibrated U_3O_8 source and aluminum absorption experiments on the active vanadium. Utilizing the radioactive decay equation,

$$dN/dt = -\lambda N \tag{1}$$

where N is the number of atoms of the radionuclide present, λ is the decay constant equal to 0.693 divided by the half life, and dN/dt is the instantaneous disintegration rate, 10^{11} atoms of active vanadium are found to exist in one liter of solution initially. This may be compared with the upper limit of vanadium in sea water of 10^{16} atoms per liter as determined spectroscopically by D. Bertrand (1942). It should be noted, however, that the experimentally determined impurity of 0.01 per cent of vanadium in the one gram of titanium metal target introduced about 10^{16} atoms of vanadium when it was diluted to 100 liters in the experiments that were undertaken.

Three possibilities existed for the mode of removal of vanadium from sea water by the ascidians. The first type would be an erratic assimilation in which no consistent variation of the remaining vanadium in the solution with time would be found. In the second case, the ascidians might concentrate constant amounts of vanadium per unit time, whereby a plot of the vanadium remaining in solution against time would give a linear relationship. Another possible mechanism would involve the ascidians concentrating the vanadium in direct proportion to the amount of vanadium present in the sea water environment. In such a case, a graph of the logarithm of the remaining amount of vanadium in the solution against time should result in a linear relationship. This last mechanism was found to be followed in experiments with *Ascidia ceratodes,* as is illustrated in Figures 1 and 2 where the logarithm of the vanadium remaining in solution (corrected for radioactive decay) is plotted against the time of withdrawal of the aliquot of sea water. In

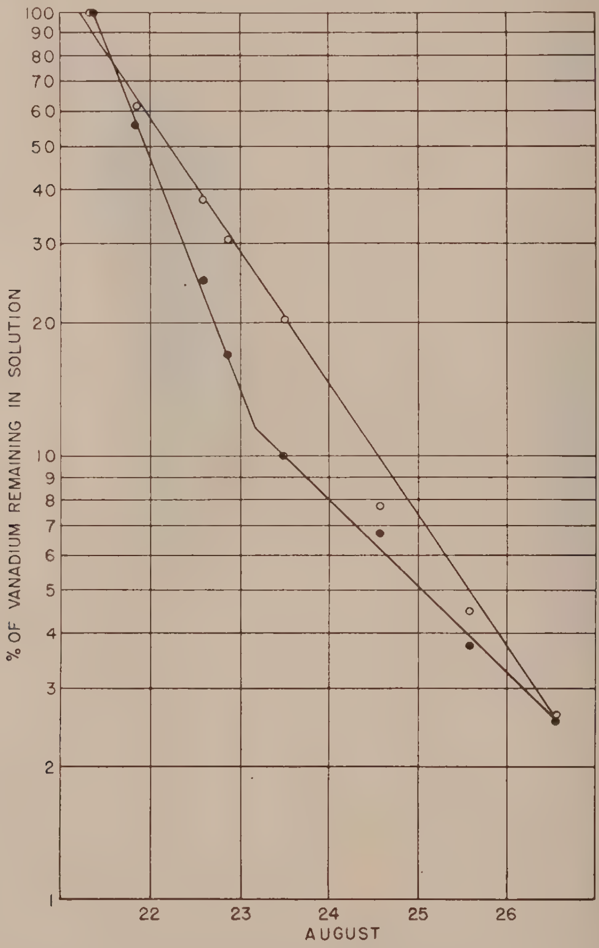

FIGURE 1. Two uptake curves of vanadium by *Ascidia ceratodes.* ○ Experiment 101. ● Experiment 2.

studies on *Ciona intestinalis* all of the curves obtained could be divided into two straight lines wherein a high initial uptake was followed by an abrupt change to a lower feeding rate. This is illustrated in Figure 2. In 10 experiments on *Ascidia ceratodes,* only two sharp changes were found in each case.

The instantaneous uptake of vanadium by these ascidians may be designated by

$$dN/dt = -VR \tag{2}$$

where V is the concentration of vanadium at time t in the sea water, N is the total amount of vanadium in the volume A of the sea water, and R is the effective clearance rate of the vanadium from the solution in units of volume per unit time, assuming a 100 per cent uptake of vanadium. It follows that

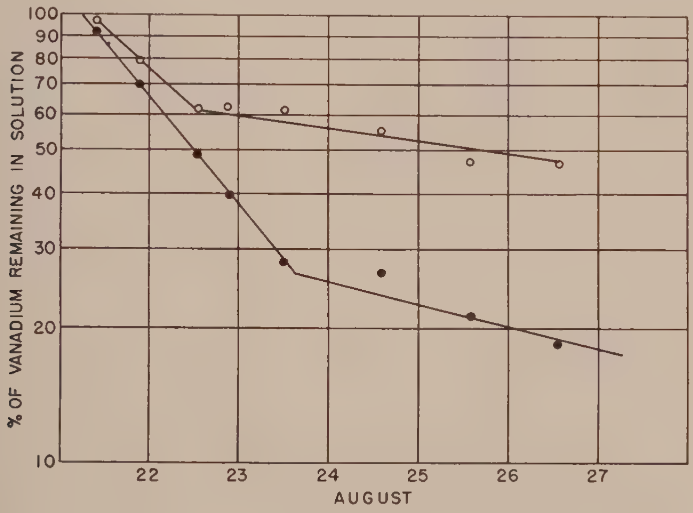

FIGURE 2. Two uptake curves of vanadium by *Ciona intestinalis.* ○ Experiment 7. ● Experiment 5.

$$V = N/A. \tag{3}$$

Utilizing Equation (3) and integrating Equation (2) from the beginning of the experiment we arrive at

$$V/V_0 = e^{-(R/A)t} \tag{4}$$

where V_0 represents the initial concentration of vanadium. For the purpose of comparative study we define the "half-time of vanadium in solution" as the time required for a given animal to reduce the vanadium concentration to half of its initial value. The values for the half-time for the 14 experiments conducted are listed in Table IV with the details of each run. Where changes occurred, the initial half-time is given.

The half-time will be a function of the effective adsorbing surface (*i.e.,* the geometry) and the rate at which the water is circulated through the animal. Where there is a change in the half-time during the course of an experiment, either or both of these parameters may change.

These experiments indicate that the initial transfer of vanadium from the hydrosphere to ascidians occurs by an adsorption process where the adsorbing surface is in an unsaturated state with respect to the adsorption of vanadium at all times, or is maintained in such a state by a constant regeneration of the surface. In either case the number of vanadium ions (or colloidal particles containing vanadium) would determine the number adsorbed at any given time.

To study more closely the dynamics of the vanadium transfer, the sea water in six experiments was enriched in phosphate ion. In the case of *Ascidia ceratodes* a high phosphate level inhibited the uptake of vanadium. This is seen in Experiments 4 and 104 where 50 microgram atoms of phosphate per liter were added initially to the sea water. In these two experiments the greatest half-times were observed. Five microgram atoms of phosphate per liter had little effect upon the uptake as is noted in Experiments 3 and 103. Since pentavalent vanadium ion can resemble phosphate ion chemically in solution, these experiments indicate that the phosphate ion competed successfully with the vanadium in the uptake process, and that vanadium in an ionic form rather than a colloidal vanadium is adsorbed. However, the solution chemistry of elements in concentrations in the level of vanadium in the sea and in our experiments has not been developed to the extent to give an unqualified answer.

TABLE IV

Half-times of vanadium in solutions containing ascidia

Experiment	Animal	Weight in Grams	Half-time Hours	Filter Treatment	Remarks
1	*A. ceratodes*	20.5 10.0	10	None	Two animals
2	*A. ceratodes*	13.5	14	Whatman 42	
3	*A. ceratodes*	23.0	24	Whatman 42	5μgr. at. $PO_4^{=}$/liter
4	*A. ceratodes*	23.2	65	Whatman 42	50μgr. at. $PO_4^{=}$/liter
101	*A. ceratodes*	29.8	24	None	
102	*A. ceratodes*	38.7	12	Whatman 42	
103	*A. ceratodes*	36.8	6	Whatman 42	5μgr. at. $PO_4^{=}$/liter
104	*A. ceratodes*	30.9	48	Whatman 42	50μgr. at. $PO_4^{=}$/liter
9	*A. ceratodes*	35.0	14	Silica column	
10	*A. ceratodes*	27.1	37	Silica column	
5	*C. intestinalis*	19.6	29	None	
6	*C. intestinalis*	25.4	22	Whatman 42	
7	*C. intestinalis*	25.6	40	Whatman 42	5μgr. at. $PO_4^{=}$/liter
8	*C. intestinalis*	47.6	18	Whatman 42	50μgr. at. $PO_4^{=}$/liter

PUMPING RATE STUDIES ON CIONA INTESTINALIS

To determine the efficiency of transfer of the vanadium from the sea water to the animals, investigations concerning the effective pumping rates of *Ciona intestinalis* were conducted. In each experiment a single animal was placed in a small plastic aquarium two inches deep (Fig. 3). A continuous flow of sea water

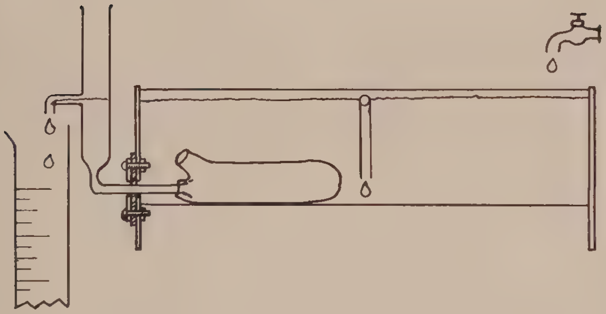

Figure 3. Aquarium used for pumping rate studies of ascidians.

was maintained and the water level was kept constant by means of drains placed at the top of the aquarium. A Pyrex glass tube of 4 mm. outer diameter with a 6 mm. outer diameter bulb at one end was inserted in the opened exhale syphon of the ascidian with great care to avoid injury to the animal. The animals soon relaxed with such an arrangement. The ascidian, with inserted tube, was then placed in the aquarium and the tube connected to a second glass tube which entered the aquarium through a rubber gasket and discharged the water outside of the aquarium at the same level as the drains. There was therefore no hydrostatic head to aid

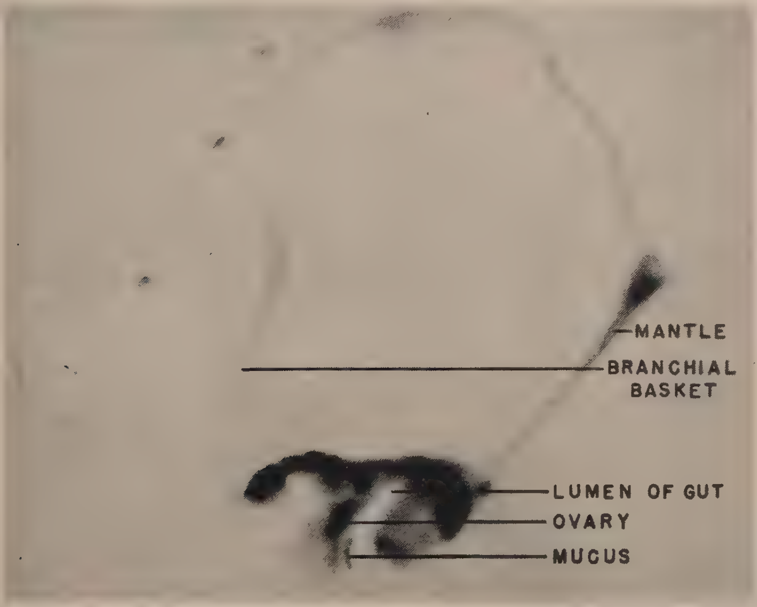

Figure 4. Radioautograph of *Ascidia ceratodes* used in Experiment 9. Concentration of vanadium is seen in ovary, gut wall, and in the mucus in the gut. Fifteen day exposure.

or hinder the ascidian in its normal pumping functions. The animals pumped at a constant rate after the tube had been inserted for two hours. The animals seemed to seal their junction to the tube by means of mucus and muscular tonus.

For an ascidian with a wet weight of 25 grams, pumping rates of about two liters per hour were observed. This result compares favorably with the pumping studies of Jørgensen (1949) on *Ciona intestinalis*; using a different technique, he obtained values of the same order of magnitude.

Radioautographic Studies

At the completion of the uptake studies with radio-vanadium the animals were sacrificed for radioautographic analysis. Both *Ascidia ceratodes* and *Ciona intestinalis* were fixed in Bouin's solution, imbedded in paraffin, and sectioned at about 100 micra. Survey autographs were obtained with Eastman No-Screen X-Ray film with exposure times up to 30 days. Figures 4 and 5 show two typical transverse sections.

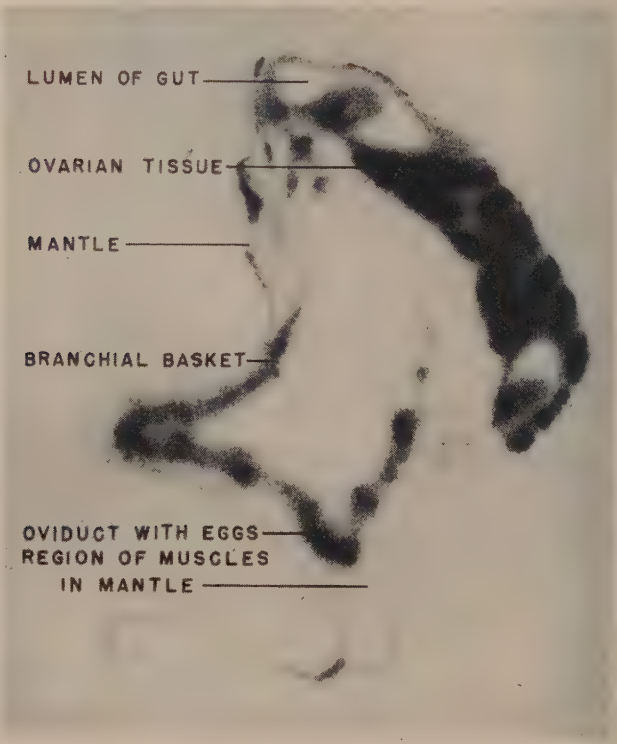

Figure 5. Radioautograph of *Ascidia ceratodes* used in Experiment 102. Concentration of vanadium is seen primarily in ovary, gut wall, oviduct (eggs), and branchial basket, with very small amounts in the mantle. No vanadium concentration was found in the muscles of the mantle. Exposure time of 15 days.

The autographs confirmed the chemical analyses on *Ciona intestinalis,* showing high concentrations in the gut wall and in the ovary, and showed similar local concentrations in *Ascidia ceratodes.* The vanadium concentration in the ovaries of both species is primarily in the follicles. The vanadium was still in the mature eggs when they were extruded from the ovary into the peribranchial cavity.

There is some concentration of the vanadium in the branchial basket of both species, though sometimes not in very great amounts. This enrichment may be due to the blood vessels in this structure, as high concentrations of vanadium in blood vessels were observed. The mantle and test showed very little vanadium and the muscles of the mantle displayed no evidence of this element. Vanadium appeared in the mucus of the branchial basket and in an isolated bit of mucus in the gut as is shown in Figure 4. The absence of high amounts of vanadium in the branchial region may have been due to washing away of the mucus sheet during the fixing procedure or to the constant renewal of fresh mucus by the living animal.

DISCUSSION

The uptake experiments establish that vanadium can be concentrated directly from solution by the two species of ascidians used in this work. To obtain an idea of the efficiency of this adsorption process, we may compare the effective clearance rate of vanadium with the pumping rates for *Ciona intestinalis.* By substitution in Equation (4) of $A = 2$ liters/hour, $V/V_0 = 1/2$, and the half time $= 30$ hours (the average from Experiments 5, 6, and 7), we arrive at an effective clearance rate of vanadium of 0.05 liters per hour. Compared with the observed pumping rate of 2 liters an hour, the efficiency of uptake of vanadium is of the order of 2½ per cent. This is the value for animals which were unfed, since food in the form of particulate matter could not be introduced without adsorbing vanadium from solution and invalidating the results.

The extraordinary biological specificity of the adsorbing surface of the ascidians for the vanadium in aqueous solution remains an unsolved problem of high biochemical interest. This selectivity is undoubtedly related to the unique ionic structure and properties of vanadium. The mucus sheet fulfills the requirement of a constantly renewed surface. The high vanadium content of the mucus, as shown by the autographs, in the branchial basket and in the gut, points to this sheet as the adsorbing surface. The sharp discontinuities in the uptake curves may be explained by chemical or area changes in the adsorbing surface.

The high concentrations of vanadium in the ovarian follicles, as shown in the autographs, suggest that this element may become part of a metabolic system that is present from the beginning in the developing embryo. Further work utilizing more concentrated radioactive vanadium solutions and thinner autograph specimens should reveal more on the intimate histology of vanadium in these animals.

We may now attempt to account for the high amounts of vanadium found in ascidians. In the case of *Ciona intestinalis* which contains about 100 micrograms of vanadium in a mature 20 gram animal, a minimum of 450 liters of sea water may be effectively cleared of vanadium in a year. This is equivalent to about 45 micrograms of vanadium. Further, we must consider that vanadium and many other elements are ionically or colloidally adsorbed on the particulate matter of the oceans. This phenomenon presented itself in the preliminary feeding experiments.

Thus, a more concentrated source of vanadium is available to these filter feeders. A final potential store of vanadium lies in the plankton of the oceans, a source of ultimate food for these filter feeding animals.

SUMMARY

1. Chemical analyses made on *Ciona intestinalis* indicated the vanadium to be localized in the gut region and the ovaries. These sites of assimilation were confirmed by radioautographs utilizing cyclotron-produced radioactive vanadium.

2. The total vanadium content of four local species of ascidians was determined. The uptake of radioactive vanadium from sea water indicated that *Ciona intestinalis* and *Ascidia ceratodes* are able, by means of an adsorption mechanism, to concentrate vanadium directly from sea water. The efficiency of assimilation was of the order of 2½ per cent for unfed animals.

3. Pumping rate of water by *Ciona intestinalis* was determined by a direct method. It was concluded that sea water and its particulate constituents could furnish the necessary vanadium demanded by *Ciona intestinalis*.

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A GIANT PHYLLOSOMA LARVA OF A LORICATE CRUSTACEAN FROM THE TROPICAL PACIFIC

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Reprinted from Transactions of the American Microscopical Society
Vol. LXX, No. 3, July, 1951

A GIANT PHYLLOSOMA LARVA OF A LORICATE CRUSTACEAN FROM THE TROPICAL PACIFIC[1]

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Introduction

During the plankton investigations made in connection with "Operations Crossroads," a remarkably large and beautiful phyllosoma larva ("glass crab") was collected at 09° 00 N 168° E in the Marshall Islands. This larva, collected by the USS Laffey on July 14, 1946, was included in a plankton haul from 950 meters to the surface.

It is not possible at this time to establish identification of the species to which the larva belongs yet it seems clear that it is a late stage in the development of a Scyllarid (square-nosed lobster). The remarkably large size, 70 mm in length, is of special interest since apparently only twice before has so large a phyllosoma been reported in the literature (Guérin, 1830, and Richters, 1873).

Von Bonde (1930) gives a brief history of the main investigations that led to the establishment of the *Phyllosoma* as larval stages of certain large Macrura, the Loricata. They were at first believed to be adult forms. Following the realization of the immature nature of these forms, a good deal of work has been done relative to establishing specific identification of the different kinds of phyllosoma larvae. Most of the larvae have been collected from the plankton. A few have been reared from the egg, thus giving a basis for exact identification of some early stages and at the same time providing a point of departure in tracing the identification of older stages of unknown types found in the plankton. The system of classification is, however, not as yet complete, as is brought out by Gurney (1936) who upon examining 400 specimens from the Discovery Expedition found that "the results are disappointing" mainly because of incompleteness of the developmental series. It is therefore worth while to contribute the following detail study of this interesting specimen.

Specimen deposited in United States National Museum.

Body

The body (Plate I) is highly transparent and leaf-like and is 70 mm in length from the tip of fore-body to tip of telson.

The *fore-body* has its greatest width anterior to the mid line and narrows only gradually forward to the anterior margin which has well defined anteriorly projecting "shoulders."

The ***hind-body*** is about two-thirds the width of the fore-body and is provided posteriorly with a deep depression in which the abdomen is attached.

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[1] Contributions from Scripps Institution of Oceanography, New Series No. 529.

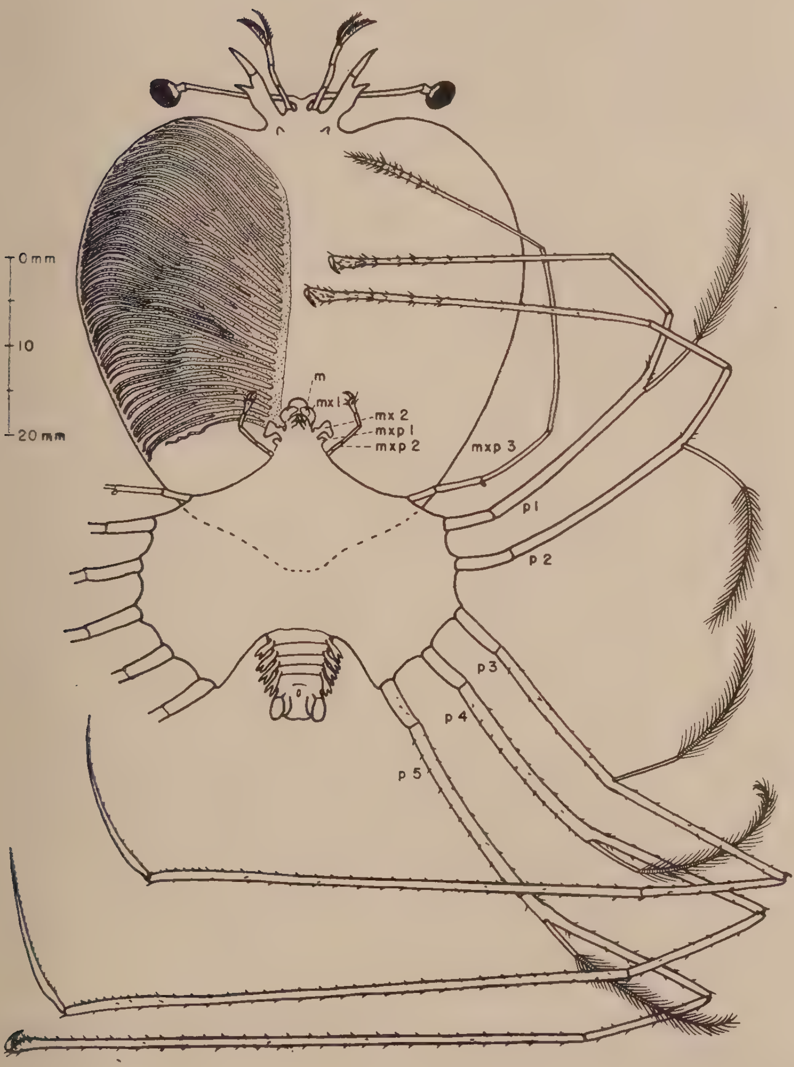
0 mm
10
20 mm
m
mx 1
mx 2
mxp 1
mxp 2
mxp 3
p 1
p 2
p 3
p 4
p 5

PLATE I

Phyllosoma larva, ventral

(Liver shown on one side only; appendages are symmetrical)

a 1—first antenna;
a 2—second antenna;
m —mandible;
mx 1, mx 2—first and second maxilla;
mxp 1, mxp 2, mxp 3—first, second and third maxilliped;
p 1, p 2, p 3, p 4, p 5—pereiopods one to five.

The *abdomen* (Plate II, Fig. 4) consists of five segments and a telson. It is relatively short and narrow and projects only a short distance beyond the posterior edge of the hind-body. Being narrow, it does not form an unbroken continuation of the lateral margins of the hind-body as in certain other Scyllarids. A short blunt spine is situated at the lateral-ventral margins on each side of the first four abdominal segments (Plate II, Fig. 4 sp.). The telson is rounded, shallowly cleft and bears no spines.

Appendages

All of the appendages but one were intact. Usually the phyllosoma taken by means of plankton nets have several of the longer appendages damaged or missing, thus depriving the investigators of useful identification characters.

First antennae (Plate II, Fig. 3, a 1). The peduncles each consist of three nearly equal segments, the third being only very slightly shorter than the first and second. The terminal rami are provided with short setae as shown in Figure 3.

Second antennae (Plate II, Fig. 3, a 2). These are blade-like and shorter than the first antennae. They each consist of two segments the first of which is broadened and at the distal end projects as a short lateral blade.

First maxillae (Plate II, Fig. 1, mx 1). These are biramous but do not possess any obvious palps such as occur in *Palinurus*.

Second maxillae and first maxilliped (Plate II, Fig. 2, mx 2 and mxp 1). These are rudimentary structures each consisting of but a single segment.

Second maxillipeds (Plate II, Fig. 2, mxp 2). There are four free segments and a terminal claw-like dactylus. The exopod is wanting.

Third maxillipeds (Plate I). These are very long and slender, each terminating in a setose dactylus. There is present a very short blunt rudimentary exopod.

Pereiopods (Plate I). The five pereiopods or legs are exceedingly long, especially the third, fourth and fifth. None of them bear gills and there is no spine on the basal segments. The endopods are fused with the preceding segment and each leg, including a well formed fifth leg, is provided with a well-developed plumose exopod. Legs one, two, and five each terminate in a short claw-like dactylus, while legs three and four have each a long sickle-shaped dactylus.

Pleopods (Plate II, Fig. 4). There are four pairs of biramous pleopods.

Uropods (Plate II, Fig. 4). These are without any spines or setae; only the outer pair appears to be articulated at the base.

Remarks

During the voyage of the COQUILLE (1882–1825) a beautiful large (70 mm) larva, *Phyllosoma laticorne*, was collected in the New Guinea area. This larva is figured in Plate 5, Figures 1 and 1A, Atlas III, and described in the accompanying text (Guérin, 1930). It appears to be of a species very near that of the present specimen but differs in that it possesses a relatively much longer abdomen, being equal in length to that of the hind-body; the first maxilliped has two lobes and the second maxilliped has a rudimentary exopod; the dactylus of the second leg is long and sickle-shaped, like that of the third and fourth legs. How many of these character differences can be ascribed to developmental stage is not known.

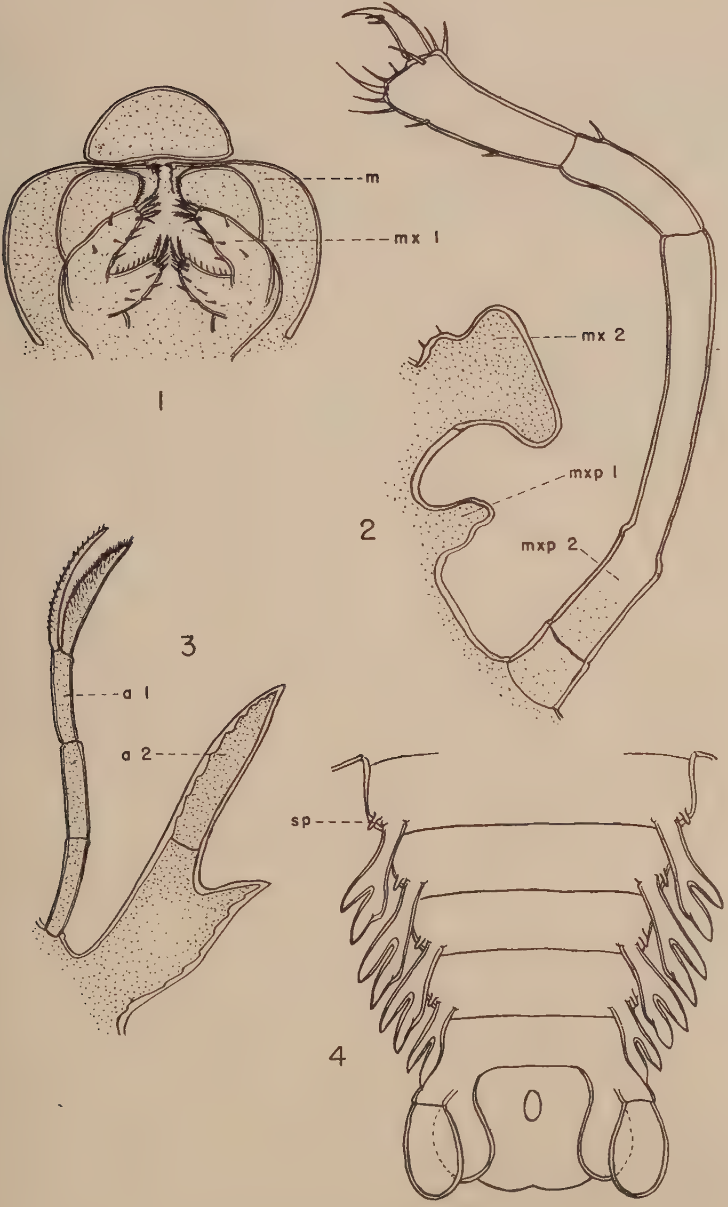

PLATE II

Phyllosoma larva

(Drawings made with the aid of a camera lucida)

FIG. 1. Mouth parts: m., mandible; mx 1, first maxilla
FIG. 2. mx 2, second maxilla; mxp 1, first maxilliped; mxp 2, second maxilliped.
FIG. 3. a 1, first antenna; a 2, second antenna.
FIG. 4. Abdomen: sp, spine.

Richters (1873) reported specimens measuring 61 and 75 mm in length, stating that these giants are dwellers in the South and East Asiatic waters and in the South Seas. His largest specimen, called *Phyllosoma longicorne*, is decidedly distinct from the present specimen in that the hind-body is broader than the fore-body and gills are present on the legs. There are also other differences. The second large specimen, *Phyllosoma indicum*, shown by Richters is quite similar to my specimen, but here too, the hind-body is relatively broader; the legs are partly missing.

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CHAPTER 8

WAVE FORECASTING AND HINDCASTING*

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INTRODUCTION

As a result of wartime research on ocean surface waves a method has been available since 1943 for the prediction of wave characteristics of interest to engineers (O'Brien and Johnson, 1947). The initial stimulus for the development came during the planning of the invasion of North Africa, and the methods subsequently devised were later used in a number of amphibious operations (Bates, 1949). The same techniques have found useful peacetime application in problems connected with coastal engineering. Much of the application to date has consisted in applying wave prediction techniques to historical rather than current meteorological data, hence the term "wave hindcasting."

The wind-generated waves in the ocean are conveniently divided into the three categories sea, swell, and surf. The term sea refers to waves under the direct influence of generating winds, and swell to waves which have left the generating area and are subject to decay in regions of weak winds or calms. The breakers which result when waves move from deep to shallow water comprise surf. The transformation of sea and swell into surf has been described in Chapter 3. With regard to prediction it suffices to mention that the computation of the shallow water characteristics from given deep water characteristics is readily accomplished from available graphs after refraction diagrams have been drawn (Hydrographic Office, 1944; Johnson, O'Brien, and Isaacs, 1948). The present discussion is confined to a brief consideration of, (1) forecasting sea and swell, (2) the significance and application of the forecast, and (3) hindcasting and its applications.

FORECASTING SEA AND SWELL

Sverdrup and Munk (1947) have obtained relationships for the growth and decay of waves by considering the energy transfer from wind to waves during growth and the reverse transfer from waves to atmosphere during decay. Empirical data have been utilized in evaluating certain coefficients and constants of integration. The growth of waves depends upon wind velocity, the duration of the wind, and the distance over which the wind blows, called fetch. Observations have shown that as the wind blows over a fetch, the wave height and period over the up-wind part shortly reach a steady state. As time passes the steady state region expands over the whole fetch. Generally, duration rather than fetch is critical in limiting wave growth. The forecasting graph which has been constructed from Sverdrup and Munk's relationships for the transient state is reproduced (Fig. 1a).

The wave height, H_F, and period, T_F, at the down-wind end of the fetch are altered by air resistance as the waves leave the fetch and decay. The change in H_F and T_F and the travel time required depend upon T_F and the decay distance D. The relationships of Sverdrup and Munk (1947) for decay have been utilized in preparing the decay graph (Fig. 1b).

The basic data required for a sea and swell forecast are wind velocity and duration, fetch, and decay distance. These data are obtained from synoptic weather maps or from weather forecasts made from such maps. The wave forecasting theory assumes that the wind velocity is constant over the fetch for the duration of the wind. In practice, this condition is never attained, and skill and judgment are

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*Contribution from the Scripps Institution of Oceanography, New Series No. 530. This work represents results of research carried out for the Office of Naval Research, Department of the Navy; and the Beach Erosion Board, Department of the Army, under contract with the University of California. The paper was largely prepared while the writer was visiting at the University of Washington, Oceanographic Laboratories.

From: Proceedings of first conference on
Coastal Engr. Long Beach, Calif.
Oct. 1950. Chapter 8. 1951.

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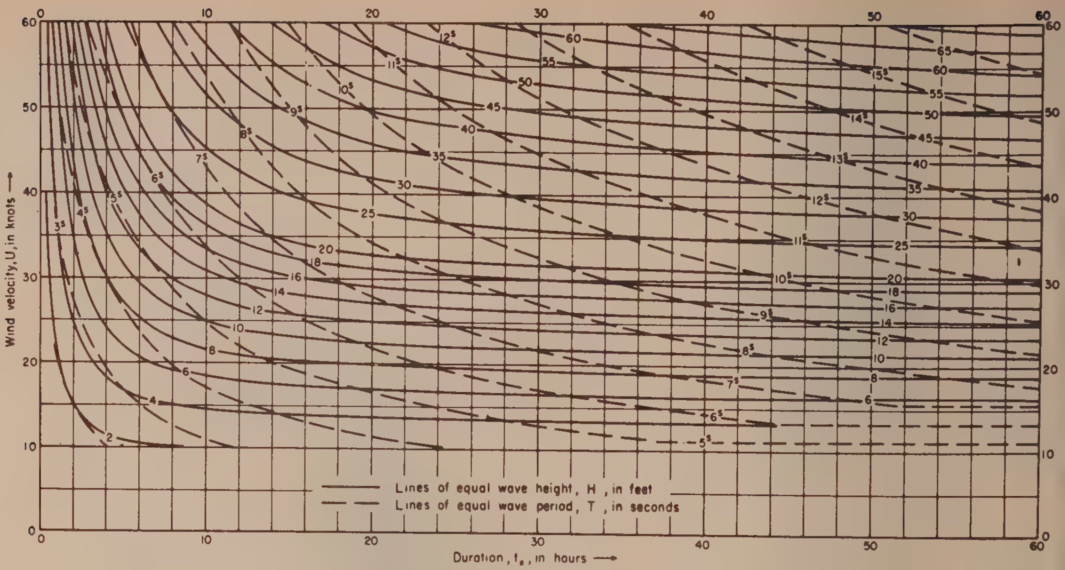


FIGURE 1a. WAVE HEIGHT AND WAVE PERIOD AS FUNCTIONS OF DURATION OF WIND AND WIND VELOCITY

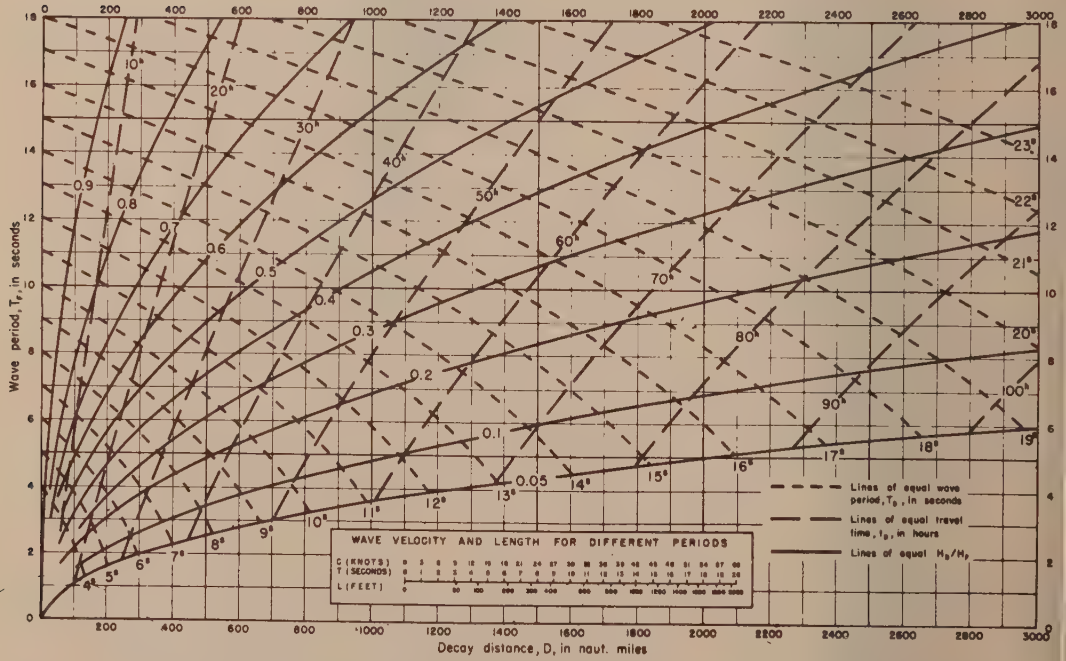


FIGURE 1b. WAVE PERIOD AT END OF DECAY DISTANCE, TRAVEL TIME, AND RATIO BETWEEN WAVE HEIGHT AT END OF DECAY DISTANCE AND AT END OF FETCH AS FUNCTIONS OF DECAY DISTANCE AND WAVE PERIOD AT END OF FETCH

required in selecting fetch, duration of the wind, and average values of wind velocity such that accurate forecasts are obtained. For this reason, persons with experience in meteorology have usually been selected for training in wave forecasting. During World War II a number of meteorologists in the armed services were trained to use the Sverdrup-Munk methods. The successful application in the field is indicated by Bates (1949), who concludes that "the techniques were basically correct and could be modified by meteorologists trained in the methods to provide reliable forecasts for amphibious operations wherever they might be held."

THE SIGNIFICANCE AND APPLICATION OF THE FORECAST

The waves in the sea are extremely complex in the sense that wave height, period, and length vary widely with respect to space and time in an apparently irregular fashion. This complexity and irregularity have made it essential to introduce statistical measures in order that wave records and observations may be characterized in a meaningful manner and the significance of the forecast be established. In many applications, only the heights and periods of the higher waves in a wave train are of practical significance. For this reason, the average height and period of the highest one-third of the waves, after ripples and waves of height less than one foot are eliminated from consideration, are useful statistical measures. These averages have been called "significant wave height" and "significant wave period," respectively (Sverdrup and Munk, 1946).

In some engineering applications, averages for the highest ten percent of the waves, or in some cases only the maximum wave height, are the important statistics. Munk (1944), Seiwell (1949), and Wiegel (1949) have determined the ratios between various statistical measures (see Table I). These ratios show variation with respect to locality and time; however, the time fluctuations at a given locality appear to be small enough so that the ratios are of great practical use.

TABLE I

Ratios of mean wave height, average of highest ten percent, and maximum height to significant wave height

	Scripps[1] (swell)	Point[2] Sur	Heceta[2] Head	Point[2] Arguello	Cuttyhunk[3]	Bermuda[3]
Interval over which averages formed	46 waves	three 20 min. intervals per day			2 minute intervals	
Ratio of mean to significant	0.67				0.64	0.64
Ratio of highest 10 percent to significant		1.27	1.30	1.30		
Ratio of maximum height to significant		1.85	1.91	1.87		

[1] Munk (1944); [2] Wiegel (1949); [3] Seiwell (1949).

The question arises as to how the wave height and period as predicted on the basis of the Sverdrup-Munk method compare with the various statistical measures. Munk (1944) has shown that the usual visual observations are best identified with significant height and period. Since visual observations were used in developing the forecasting method, it would appear that predicted wave heights and periods might be considered to be significant heights and periods. Isaacs and Saville (1949) have demonstrated that this is the case by a comparison of predicted heights and periods with significant heights and periods extracted from records made at several west coast stations. Preliminary indications show the same results for a study on the east coast sponsored by the Beach Erosion Board (James, 1951).

The investigations described in this section serve to indicate the significance of the wave forecast with respect to the actual waves occurring in the sea.

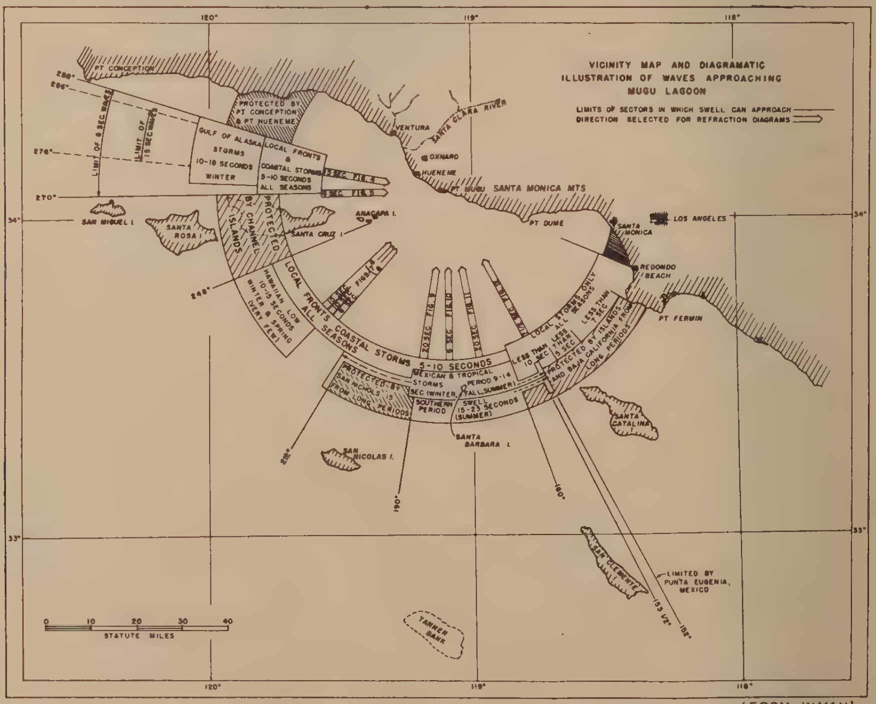
Ratios such as those given in Table I are extremely important in this regard. For application in problems of sand erosion during construction of coastal works, predictions of significant wave height and period may be desirable. On the other hand, in problems of structural strength under wave action, predictions of the maximum wave height are needed. Wave forecasting has advanced to a stage where it is possible in many localities to furnish useful predictions of the various wave characteristics to engineers engaged in the construction of coastal works.

HINDCASTING AND ITS APPLICATIONS

Because of the lack of wave records or adequate visual observations of waves in many regions, there has been a demand for wave data obtained by hindcasting (Burt and Sauer, 1948). Accumulated wind data are generally sufficient for most localities in the Northern Hemisphere to permit computation by means of the forecasting method of past wave characteristics. In particular, the Daily Synoptic Series, Historical Weather Maps, Northern Hemisphere, have been found most useful in this regard (see Chapter 10).

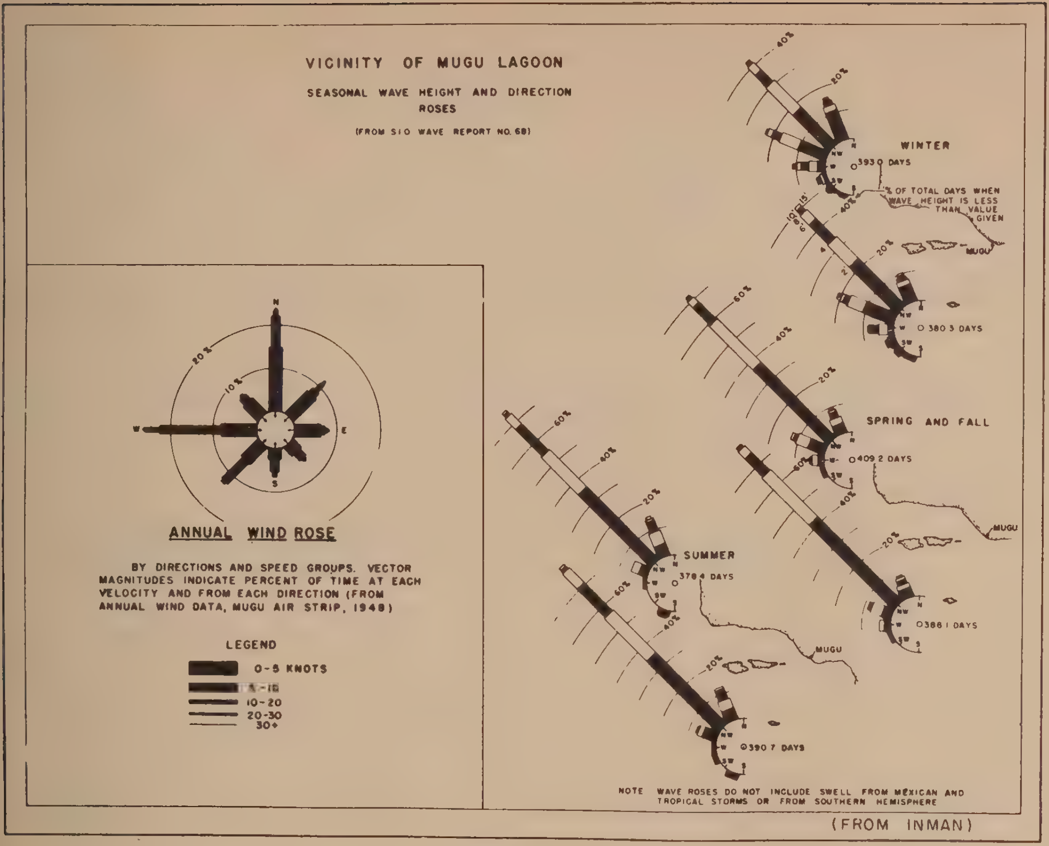
The hindcasting technique can provide statistical wave data over a large area in a short period of time. In one application for the Corps of Engineers, Los Angeles District, two forecasters and three clerks computed in about four months, the deep-water wave characteristics over a three-year period for the California Coast (Scripps Institution of Oceanography, 1947). The cost of such data is not large relative to the cost of installing and maintaining wave meters and analyzing the resulting records over a three-year period.

Such data have proven useful in providing a basis for the design of coastal structures such as off-shore drilling installations. Use has also been made in examining the question of the stability of beaches prior to construction of coastal works. Inman (1950) has used wave data provided by the hindcasting technique in a coastal beach study in the vicinity of Mugu Lagoon, California, and two illustrations are reproduced from his report. Fig. 2 shows the sources and period ranges for waves approaching the coast near Mugu Lagoon from various directions. Fig. 3


VICINITY MAP AND DIAGRAMATIC
ILLUSTRATION OF WAVES APPROACHING
MUGU LAGOON
LIMITS OF SECTORS IN WHICH SWELL CAN APPROACH
DIRECTION SELECTED FOR REFRACTION DIAGRAMS
120°
119°
118°
34°
33°
PT CONCEPTION
288°
286°
276°
270°
248°
212°
190°
160°
LIMIT OF 8 SEC WAVES
LIMIT OF 15 SEC WAVES
PROTECTED BY PT CONCEPTION & PT HUENEME
GULF OF ALASKA STORMS 10-18 SECONDS WINTER
LOCAL FRONTS & COASTAL STORMS 5-10 SECONDS ALL SEASONS
15 SEC FIG. 4
8 SEC FIG. 5
VENTURA
SANTA CLARA RIVER
OXNARD
HUENEME
PT MUGU
SANTA MONICA MTS
PT DUME
SANTA MONICA
LOS ANGELES
REDONDO BEACH
PT FERMIN
SAN MIGUEL I.
SANTA ROSA I.
SANTA CRUZ I.
ANACAPA I.
PROTECTED BY CHANNEL ISLANDS
HAWAIIAN LOW 10-15 SECONDS WINTER & SPRING (VERY FEW)
LOCAL FRONTS ALL SEASONS
COASTAL STORMS 5-10 SECONDS
FIGS. 7 & 8
20 SEC FIG. 9
8 SEC FIG. 10
20 SEC FIG. 11
LOCAL STORMS ONLY ALL SEASONS
LESS THAN 10 SEC
LESS THAN 5 SEC
LESS THAN 7 SEC
PROTECTED BY ISLANDS AND BAJA CALIFORNIA FROM LONG PERIODS
MEXICAN & TROPICAL STORMS PERIOD 9-14 SEC (WINTER, FALL, SUMMER)
SOUTHERN SWELL PERIOD 15-23 SECONDS (SUMMER)
PROTECTED BY SAN NICHOLS IS FROM LONG PERIODS
SANTA BARBARA I.
SAN NICOLAS I.
SANTA CATALINA I.
SAN CLEMENTE
LIMITED BY PUNTA EUGENIA, MEXICO
TANNER BANK
0 10 20 30 40
STATUTE MILES

(FROM INMAN)

Fig. 2



(FROM INMAN)

Fig. 3

shows seasonal wave height and direction roses for a three-year period for the portion of the coast near Mugu Lagoon. The source material for both figures was obtained by an examination of past meteorological situations and hindcasting from historical weather maps.

Hindcasting has also been useful in providing information on the characteristics of waves which have caused failures in coastal installations (Horrer, 1950). In the past, adequate records have often not been kept of the wave conditions associated with such failures even though the damage has been carefully noted. Hindcasting can help fill in the gap in order that future designs may be improved.

Finally, it is to be emphasized that although hindcasting is a useful technique for providing wave data it should supplement rather than supplant wave records and observations. Every individual hindcast is subject to the uncertainties contained in the forecasting method, and may, therefore, be in error compared to the actual wave conditions. In the statistical accumulation of many hindcasts these errors tend to compensate, but the security of the results must always depend ultimately on comparison with actual observations.

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CHAPTER 1

ORIGIN AND GENERATION OF WAVES*

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INTRODUCTION

It is no more possible to speak of _the_ origin of ocean waves than it is to speak of _the_ origin of sound waves, or of electromagnetic waves. Different types of waves exist, often simultaneously, and these differ from one another with respect to their origin and generation.

A convenient classification can be made on the basis of wave period, i.e., the time interval between the passage of successive crests at a fixed point. Tentatively we may use the following major divisions (Fig. 1):

Classification	Period
Capillary waves	less than 0.1 sec.
Ultra-gravity waves	from 0.1 sec. to 1 sec.
Ordinary gravity waves	from 1 sec. to 30 sec.
Infra-gravity waves	from 30 sec.to 5 min.
Long-period waves	from 5 min. to 12 hours
Ordinary tides	12 hours to 24 hours
Trans-tidal waves	24 hours and up

These ranges correspond to bands in the spectrum of electromagnetic waves and altogether constitute the _spectrum_ of ocean waves.

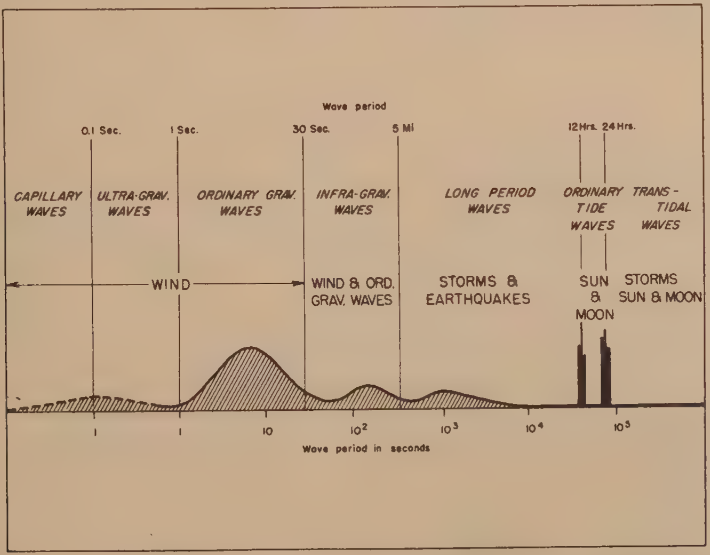

Fig. 1. Tentative classification of ocean waves according to wave period. The forces responsible for various portions of the spectrum are shown. The relative amplitude is indicated by the curve.

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[1] *Contribution from the Scripps Institution of Oceanography, New Series No. 531. This work represents results of research carried out for the Office of Naval Research, Department of the Navy, and the Beach Erosion Board, Department of the Army, under contract with the University of California.

From: Proceedings of first conference on
Coastal Engr. Long Beach, Calif.
Oct. 1950. Chapter 1. 1951.

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APPLICATION OF SPECTRUM

Virtually all the energy of the spectrum is contained in two of the period ranges: the ordinary gravity waves, and the ordinary tides. These are the ones that can be noticed with the naked eye, the ones that have affected mankind since the dawn of history. In the minds of this group the term "waves" is virtually synonymous with the ordinary gravity waves, and we shall be concerned chiefly with them.

However, it is not just for academic reasons that the entire spectrum is discussed. There are some engineering applications that are definitely concerned with periods other than those of the ordinary gravity waves or the tides. The reason usually has to do with "resonance." For example, an artificial harbor with a natural period of oscillation of 2 min. may develop troublesome 2-min. surges, and these depend largely on infra-gravity waves, even though these waves are only a few inches high and completely obscured by much higher waves of shorter period. A ship with a natural roll of 5-sec. period is greatly affected by waves of about 5-sec. period, but only slightly affected by a 14-sec. swell, even though the swell may be much higher. The effectiveness of RADAR is limited by "sea clutter" due to reflection and scatter from capillary waves, rather than the higher wind waves. There are other examples, and they will be covered in the following chapters.

THE STUDY OF THE WAVE SPECTRUM

The scientific problem is to study the origin of the entire wave spectrum, and, as a final test of such efforts, to predict it. Once the spectrum is known, it is the problem of the engineer to evaluate its effect on engineering structures, harbors, and many other things. There has been considerable success in predicting tides, and for most practical application these predictions are adequate. There has been moderate success in predicting wind waves and swell. This subject is discussed by R. S. Arthur in Chapter 8. Briefly reviewed below is the little that is known regarding the fundamentals of wave generation, starting with the waves of shortest period.

CAPILLARY WAVES

This portion of the spectrum is affected to a larger extent by surface tension than by gravity. Very roughly we may include waves of periods less than 0.1 sec. The appropriate wave lengths are shorter than one inch. The velocity increases with decreasing period and length, but always exceeds 0.75 ft. per sec.

These waves are caused by wind, but we know nothing of their mode of origin. They are greatly affected by surface-active agents, such as oils and detergents. They are rapidly damped by viscous forces, and apparently require winds above 3 ft. per sec. for their generation. These waves determine largely the optical effects of the surface. One convenient way of studying them is to photograph the glitter of the sun on the water surface. These capillary waves are also largely responsible for what might be termed the inherent roughness of the surface. As such they determine the effectiveness with which the wind can grip the water. This in turn enters in the study of currents, the piling up of water by on-shore winds (storm tides), and also in the generation of longer period waves.

ULTRA-GRAVITY AND ORDINARY GRAVITY WAVES

Again we deal with waves which owe their existence to the wind. Two mechanisms by which the wind may cause these waves to grow are, (a) an excess in pressure on the windward side of waves compared to the pressure on the leeward side, (b) tangential drag on the water surface, assuming waves to have a mass transport according to the irrotational theory. These are the two mechanisms which form the basis of the forecasting method described in Chapter 8. They are of about equal magnitude. There are a number of other possible mechanisms for explaining wave growth, and some of these are now being investigated. All these processes already require the existence of a wave, though possibly one of very small height, in order for the wind to transfer energy to it and to make it grow. However, such a distinction between "origin" and "growth" does not appear to be of practical importance. It seems safe to assume that the impulses received by the sea surface as a consequence of the gustiness of the wind assures a steady supply of very low waves of all length.

The outstanding weakness of present theories concerning the generation of waves is that they do not allow for the variability of the ordinary gravity waves. The theories are concerned only with the higher waves present. They say nothing about the character of the waves twice the period of the higher waves, or half their period.

Consider a rather severe storm, capable of raising a sea for which the higher waves are 20 ft. high and have a period of 10 sec. At the same time there will be present longer waves and shorter waves. The longest waves may have periods up to 25 sec. The height of the 20-sec. waves is perhaps only one foot, and to the naked eye these long waves are obscured by the higher waves present. Owing to the fact that in deep water the velocity of the waves is proportional to their period, these long waves will travel ahead of the heavy swell and may reach land several days prior to the arrival of the highest waves. The practical application of these "forerunners" of the swell in providing a warning of higher waves to come (and possibly the storm itself) has been demonstrated in the Atlantic and Pacific.

Measurements of swell, and forerunners of swell, indicate a remarkably slow attenuation of these waves after they have left the storm area. We are recording in California waves from violent storms in all parts of the Pacific to which we are exposed. As a matter of fact, our heavy summer swell has its origin in the roaring forties of the South Pacific Ocean, 5000 miles and 10 days travel time removed from here. Some allowance for a decrease in wave height and a shift towards the longer periods has been made in existing theories. Measurements at Oceanside, California by the Department of Engineering, University of California, Berkeley, indicate that the present estimates of period increase in swell are in error (Wiegel and Kimberley, 1950).

INFRA-GRAVITY WAVES

Instruments especially adapted for the recording of the long waves have revealed the presence of 2-min. waves that are related to the variability in the incoming ordinary gravity waves. A series of high breakers temporarily raises the water level, a series of low breakers permits the level to fall. This oscillation (surf-beat) appears to be propagated seaward from the surf zone. Just outside the surf zone the amplitude of the surf-beat is 10 percent of that of the mean breakers.

These long waves in their travel seaward are greatly affected by the bottom topography over the entire continental shelf. Isaacs, Williams, and Eckart (1951) have shown that they may even be turned around completely and returned to shore. Calculations show that in depths of several hundred feet the orbital velocities near the bottom associated with the surf beat is likely to be larger than the corresponding velocities of the incoming ordinary gravity waves. A pipe line along the bottom at such depths would be affected principally by such long-period waves. Oscillations in bays and harbors (seiches) may be the result of surf beat.

LONG-PERIOD WAVES

Fairly well defined waves of 15- to 20-min. periods have also been recorded at La Jolla and Oceanside, California. The origin of these waves remains obscure, although a correlation with the meteorological situations is strongly indicated. Some of the remarks made in relation to the surf beat apply here also. These waves are small, hardly more than 2 in. in amplitude.

Waves of somewhat the same period, but of much larger height, result from the sudden displacement of the sea bottom during submarine earthquakes. Popularly these are known as "tidal waves," but since they have nothing to do with the tides, we prefer to use the Japanese word "tsunamis." In Hilo, Hawaii, a tsunami of destructive intensity seems to come about once every 20 years. Protection against such tsunamis is certainly the No. 1 problem of coastal engineering in the Hawaiian area. The construction of a 15 ft. sea wall along the waterfront in Hilo is now being seriously considered. Fortunately the coast of Southern California does not seem to be subject to destructive tsunamis. The largest tsunami waves here that have come to my attention were recorded in the Mission records of San Diego: 2.5 ft

ORDINARY TIDES

These are caused by the sun and moon. As a whole, the two contribute about equally, since the very much larger mass of the sun is just about compensated for by its larger distance. Most of the energy goes into the semi-diurnal and diurnal periods (the "ordinary" tides), and these are of the same order of magnitude along our coast as the ordinary gravity waves. In most instances, but not always, the effect of the wind on waves of ordinary tide period is relatively small, and the forecast based only on the astronomic factors is satisfactory. It should be added that the forecasts are largely empirical: only the periods of the components are computed from astronomical considerations, whereas the amplitude and phase of each component is determined from tide records at or near the locality for which the forecast is made.

TRANS-TIDAL WAVES

There are various components of solar and lunar tides in this range of periods but these tend to be outweighed by the meteorologic factors. The situation is therefore reversed from what is found in the ordinary tide range.

In the river Thames non-tidal variations in water level of several days duration have been observed. There seems to be a correlation between such variations and the passage of storms over the Wyville Thompson ridge in the North Atlantic.

There are also seasonal variations in water level related to the variations in ocean current, and hence indirectly to the prevailing winds. It is not generally known that along the coast of Southern California the mean sea level in the summer is 2/3 of a foot above that in the winter.

We could go on, and consider variations in sea level that have taken place in climatic cycles. For example, the oceans are believed to be rising 1/2 foot per century.

CONCLUSIONS

Any shore installation is, therefore, under the influence of waves ranging in periods from milliseconds to years. The underlying causes of these waves are the winds, directly or indirectly; the sun and moon, and submarine earthquakes. By far the largest part of the spectrum reflects the action of the wind. The wind is most effective in raising waves whose periods lie between 5 sec. and 15 sec. These can be predicted, in a manner. The fact that shorter and longer waves are of smaller height does not mean that they are of no practical consequence. In 10 to 20 years we may be able to predict the entire spectrum of wind generated waves.

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Chapter 5

NEARSHORE CIRCULATION*

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INTRODUCTION

Studies of nearshore circulation were initiated at Scripps Institution during World War II. A method of estimating the velocity of longshore currents from known wave conditions on straight beaches with parallel contours was devised by Munk and Traylor (1945) and later revised by Putnam, Munk and Traylor (1949). Their methods were based on energy and momentum considerations which were applied to the following two types of observations: (1) field observations of longshore currents along the straight beach at Oceanside, California made by Munk and Traylor (1945), and (2) laboratory measurements conducted at the Department of Engineering, University of California.

In 1945 a program of field observations was initiated to study the nearshore currents in relation to a variety of coastal types and submarine configurations. Operations extending over a period of one year involved measurement of currents inside the breakers at 63 stations from the United States -- Mexican boundary to Newport, California (Shepard, 1950) (Fig. 1). The observations were repeated approximately every 12 days. Subsequently the shallow waters adjacent to individual beaches representative of various types of environment have been studied intensively. This work has included a beach with adjacent submerged ridge and canyon topography (Shepard and Inman, 1950), two straight beaches with parallel bottom contours, and one beach at the head of a crescentic bay. In addition the effects of jetties, piers, and points have been investigated. During this work currents inside and outside the breaker zone were investigated. Most of the observations were made in southern California, but studies along many other coasts of the United States and in the Hawaiian Islands indicate that the results have a general application.

All devices used in these investigations were of a free drifting type, the velocity being determined by the distance of travel in a given period of time. Currents outside of the surf zone were measured by surface floats, dye, and triplanes (current crosses) submerged at a variety of depths. Locations were obtained by multiple sextant angles from accompanying boats. Inside the breaker line bottom currents were measured by volley balls given slight negative buoyancy. Surface currents were observed by free floating kelp and dye. Details of the methods are given by Shepard and Inman (1950). Wave recordings were obtained simultaneously with many of the measurements. Angles of wave approach were determined in part by the transit-sighting bar method devised by Forrest (1950).

TERMINOLOGY AND GENERAL PRINCIPLES OF CIRCULATION

Observations of nearshore circulation show that there are certain basic principles which apply to most environments, including in varying degree straight beaches with parallel offshore contours and beaches adjoined by irregular submarine topography. There appear to be at least two interrelated current systems (Fig. 2):

1. The coastal currents which flow roughly parallel to the shore, and constitute a relatively uniform drift in the deeper water adjacent to the surf zone. These currents may be tidal currents, transient wind-driven currents, or currents associated with the distribution of mass in local waters.

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*Contribution from the Scripps Institution of Oceanography, New Series No. 532. This work represents in part research carried out for the Beach Erosion Board and the Office of Naval Research under contracts with the University of California.

From: Proceedings of first conference on
Coastal Engr. Long Beach, Calif.
Oct. 1950. Chapter 5. 1951.

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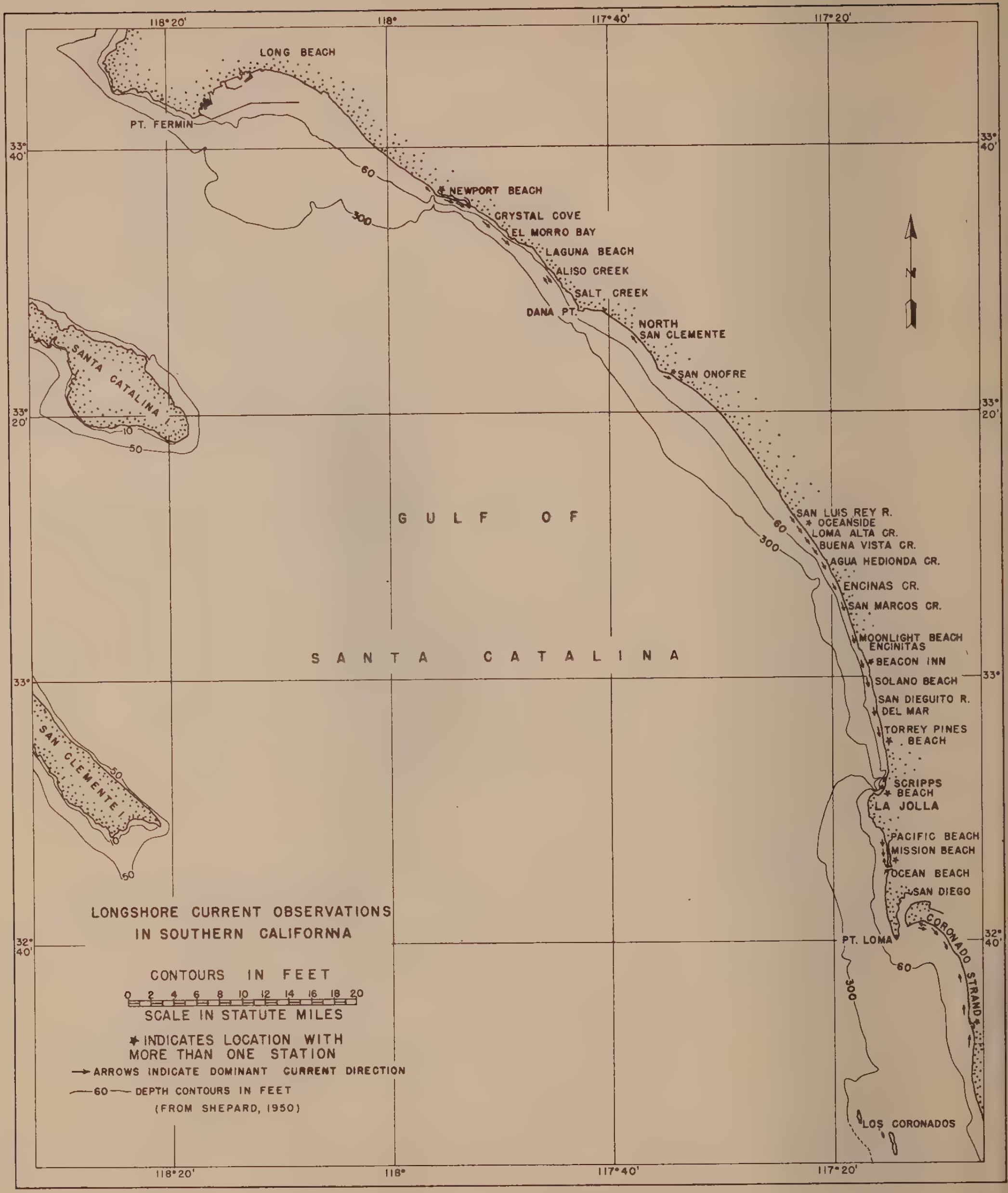
118°20'
118°
117°40'
117°20'
33° 40'
33° 20'
33°
32° 40'
LONG BEACH
PT. FERMIN
60
300
NEWPORT BEACH
CRYSTAL COVE
EL MORRO BAY
LAGUNA BEACH
ALISO CREEK
SALT CREEK
DANA PT.
NORTH SAN CLEMENTE
SAN ONOFRE
N
SANTA CATALINA I.
10
50
GULF OF SANTA CATALINA
SAN CLEMENTE I.
SAN LUIS REY R.
OCEANSIDE
LOMA ALTA CR.
BUENA VISTA CR.
AGUA HEDIONDA CR.
ENCINAS CR.
SAN MARCOS CR.
MOONLIGHT BEACH
ENCINITAS
BEACON INN
SOLANO BEACH
SAN DIEGUITO R.
DEL MAR
TORREY PINES BEACH
SCRIPPS BEACH
LA JOLLA
PACIFIC BEACH
MISSION BEACH
OCEAN BEACH
SAN DIEGO
CORONADO STRAND
PT. LOMA
LOS CORONADOS
LONGSHORE CURRENT OBSERVATIONS IN SOUTHERN CALIFORNIA
CONTOURS IN FEET
0 2 4 6 8 10 12 14 16 18 20
SCALE IN STATUTE MILES
✱ INDICATES LOCATION WITH MORE THAN ONE STATION
→ ARROWS INDICATE DOMINANT CURRENT DIRECTION
—60— DEPTH CONTOURS IN FEET
(FROM SHEPARD, 1950)

Fig. 1
Showing areas where nearshore current measurements have been made in southern Cali

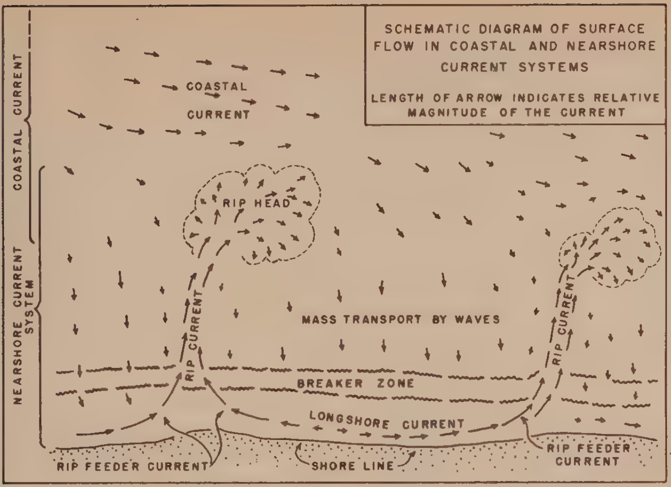
SCHEMATIC DIAGRAM OF SURFACE FLOW IN COASTAL AND NEARSHORE CURRENT SYSTEMS
LENGTH OF ARROW INDICATES RELATIVE MAGNITUDE OF THE CURRENT
COASTAL CURRENT
COASTAL CURRENT
NEARSHORE CURRENT SYSTEM
RIP HEAD
RIP CURRENT
RIP CURRENT
MASS TRANSPORT BY WAVES
BREAKER ZONE
LONGSHORE CURRENT
RIP FEEDER CURRENT
SHORE LINE
RIP FEEDER CURRENT

Fig. 2

2. A nearshore system which may be superimposed on the inner portion of the coastal current or in the absence of a coastal current may exist indepently. The nearshore system is associated with wave action in and near the breaker zone and consists of: (a) shoreward mass transport of water due to wave motion, which carries water through the breaker zone in the direction of wave propagation, (b) movement of this water parallel to the coast as longshore currents, (c) seaward return flows, such as flow along concentrated lanes known as rip currents, and (d) longshore movement of the expanding head of the rip current.

Since the rip currents have relatively high offshore velocities, the shoreward movement is restricted to wide lanes in between rip currents. As a result, the circulation pattern takes the form of an eddy or cell with a vertical axis (Fig. 2). The positions of shoreward motion and seaward return are much dependent on the submarine topography, the configuration of the shoreline, and the height and period of the waves. Periodicity or fluctuation of current velocity and direction is a characteristic of flow in the nearshore system (Shepard and Inman, 1950). This variability is primarily due to the grouping of high waves followed by low waves, a phenomenon which gives rise to surf beat (Munk, 1949b).

The direction of longshore current is primarily dependent on two factors: (1) the direction of wave propagation, and (2) the rise in water level due to the shoreward mass transport of the waves, which is greatest in the zones of highest breakers along a beach (wave convergence zones). The longshore currents commonly flow away from these zones of highest waves.

There may be processes other than rip currents by which water may be returned seaward (Munk, 1949a). Our observations indicate the importance of a net seaward drift along the bottom inside the breaker zone and a net shoreward movement at the surface. Comparisons of the offshore and onshore components of surface and bottom currents in the surf zone are given in Table I. This table shows that there is a definite tendency for bottom longshore currents to have a small offshore component. The lack of a pronounced onshore component for the surface currents is probably due to the method of observation (see footnote to Table I on following page).

To date we have not found any indication that these differential net movements between top and bottom extend any distance outside of the breaker zone, but rather that the current moves shoreward from top to bottom in one area and seaward from top to bottom in another outside of the breaker zone.

TABLE 1

Comparison of the offshore and onshore tendencies between surface and bottom currents in the surf zone. Based on all observations, irrespective of magnitude.

Location	Surface Currents[1]			Bottom Currents[2]		
	No. of Obs.	% Offshore	% Onshore	No. of Obs.	% Offshore	% Onshore
Torrey Pines Beach Pacific Beach Mission Beach	139 162 224	54.7 47.5 50.0	45.3 52.5 50.0	512 220 383	81.4 81.8 76.3	18.6 18.2 23.7
Total No. of Obs.	525			1115		
Average %		50.5	49.5		79.7	20.3

[1] Surface currents were measured by free floating kelp and dye and thus represent measurements of a relatively thick surface layer and not the surface itself which is known to have a greater onshore tendency (Shepard and Inman, 1950, p. 200).

[2] Bottom currents were measured with volley balls given slight negative buoyancy.

STRAIGHT BEACHES WITH PARALLEL CONTOURS

Most beaches have some curvature and the adjacent bottom topography is usually somewhat irregular. However, there are a sufficient number of beaches which are essentially straight with parallel bottom contours to warrant consideration. This type of beach is ideal for theoretical treatment and was therefore chosen for the investigations of longshore currents by Putnam, Munk and Traylor (1949). Their momentum approach has been widely used. It relates the velocity V, of the longshore currents to the wave height H, period T, angle of approach α, and slope i of the beach, according to the equation:

$$V = \frac{a}{2}\left[\sqrt{1 + \frac{4C\,\sin\alpha}{a}} - 1\right] \qquad (1)$$

where

$$a = (2.61\ i\ H\cos\alpha)\ /\ (kT)$$

and, $C = \sqrt{2.28\ g\ H}$ is the wave velocity, k is the beach friction coefficient (hydraulic roughness), and g is the acceleration of gravity.

Field measurements partly reported by Shepard (1950) have indicated only partial agreement with current velocities predicted from the equation. The discrepancies appear to be due to:

1. Rip currents which normally increase the flow in the dominant direction on the up current side of the rip zone and decrease or reverse the current on the other side (Fig. 3).
2. Cell-like circulation of the nearshore system, which exists even under conditions of normal wave approach (breaker crests essentially parallel to the beach). According to the formula there should be no current under conditions of normal approach. However, with large breakers longshore currents of velocity of one or more knots have been observed for limited distances despite this normal approach.
3. The fluctuating nature of longshore currents which requires measurements over a long interval of time in order to obtain an average that is suitable for comparison with the predicted value.

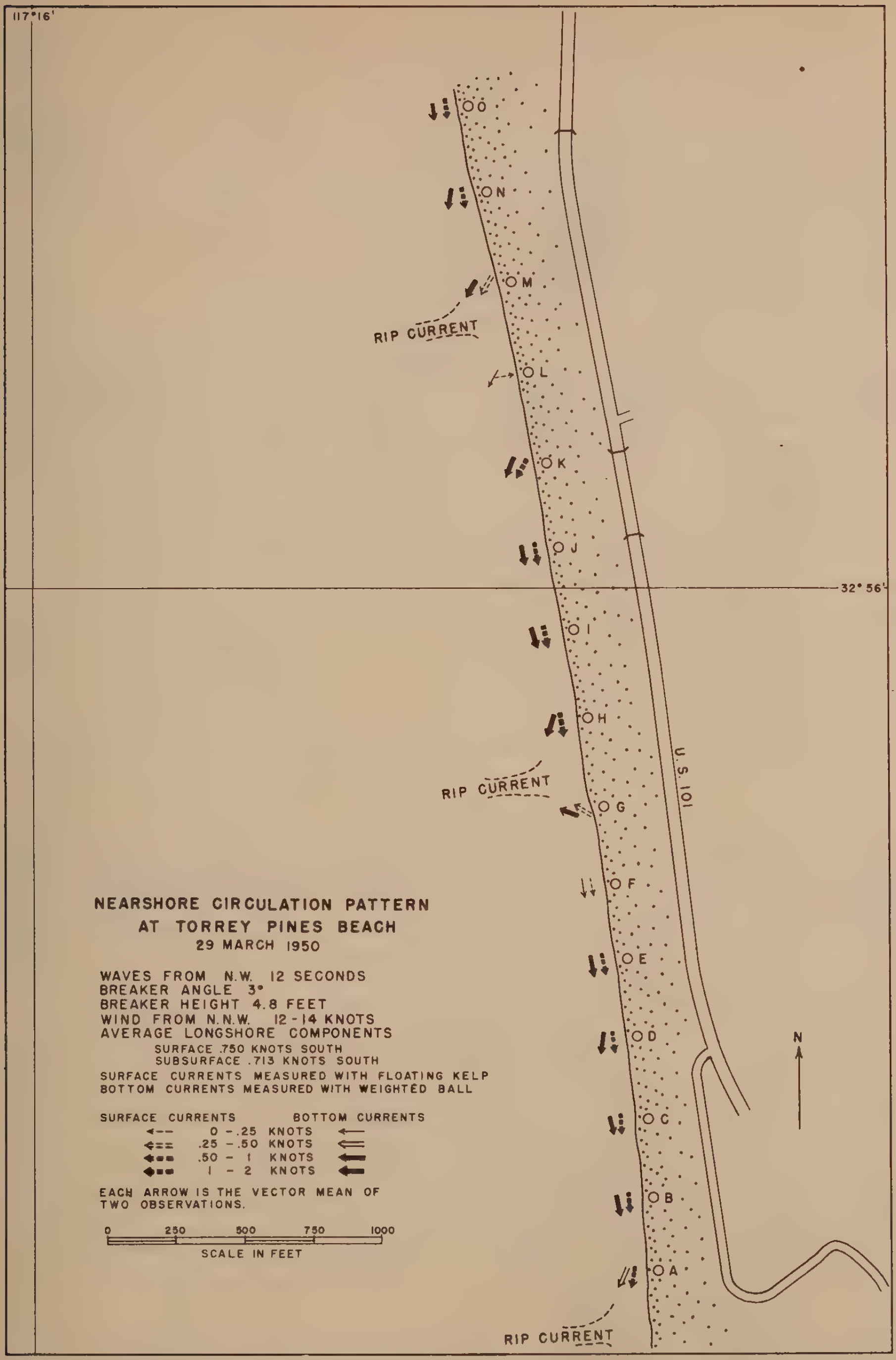
117°16'
32° 56'
O O
O N
O M
RIP CURRENT
O L
O K
O J
O I
O H
RIP CURRENT
O G
O F
O E
O D
O C
O B
O A
RIP CURRENT
U.S. 101
N
NEARSHORE CIRCULATION PATTERN
AT TORREY PINES BEACH
29 MARCH 1950
WAVES FROM N.W. 12 SECONDS
BREAKER ANGLE 3°
BREAKER HEIGHT 4.8 FEET
WIND FROM N.N.W. 12-14 KNOTS
AVERAGE LONGSHORE COMPONENTS
SURFACE .750 KNOTS SOUTH
SUBSURFACE .713 KNOTS SOUTH
SURFACE CURRENTS MEASURED WITH FLOATING KELP
BOTTOM CURRENTS MEASURED WITH WEIGHTED BALL
SURFACE CURRENTS
BOTTOM CURRENTS
0 - .25 KNOTS
.25 - .50 KNOTS
.50 - 1 KNOTS
1 - 2 KNOTS
EACH ARROW IS THE VECTOR MEAN OF TWO OBSERVATIONS.
0
250
500
750
1000
SCALE IN FEET

Fig. 3
Showing the influence of circulation pattern and rip currents on the direction and magnitude of longshore currents on a straight beach. Note that in the lee of rip current zones the longshore current is much reduced (station L) and sometimes reversed in direction (station G).

4. The fact that beach friction coefficient (k) was assumed to be a constant for a given beach. Further measurements indicated that it is a function of current velocity (Fig. 4).

5. Many beach approaches are terraced, making application of the formula impossible.

The nearshore circulation is frequently the result of waves approaching the coast from more than one direction, making current predictions extremely difficult.

Despite these discrepancies the longshore currents outside straight beaches with parallel submarine contours appear to be essentially the result of the factors considered by Putnam, Munk and Traylor (1949).

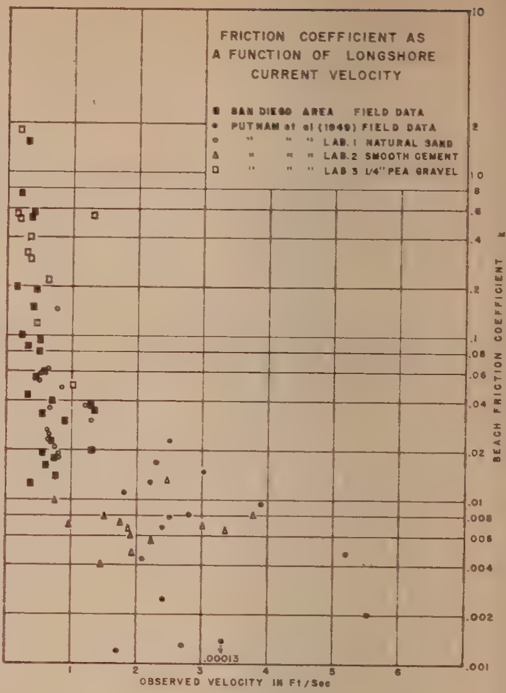

Fig. 4

The average longshore component of currents observed along two relatively straight beaches with parallel bottom contours in the San Diego area were compared with the currents predicted from equation 1. Preliminary plotting of the observed versus the computed velocity showed a rather large scatter, the amount of disagreement apparently being a function of the velocity of the current. This suggested the possibility that the friction coefficient, k, is not a constant for a given beach, but varies with the velocity.

Using the observed value of the longshore current, the value of k was computed for all of the field and laboratory observations listed in Putnam et al (1949) and for those recently obtained in the San Diego area. The coefficient k is plotted as a function of the observed velocity in Fig. 4. Inspection of this figure strengthens the contention that the coefficient k is a function of velocity, particularly for values of current of the order of two feet per second and less. Predicted values of longshore current based on k values from Fig. 4 have shown good agreement with field observations.

The regular spacing between rip channels cutting through the longshore bars along the straight, fine-sand beaches of northern Oregon and southern Washington indicates that the general features of the nearshore circulation pattern described in this report also apply to these northern beaches. At low tide the distance between rip channels can easily be ascertained from car speedometer readings. Observations of this type were made along the straight beaches of Clatsop Spit, Oregon, and Leadbetter Spit, Washington, on the 17th and 18th of June, 1950. The mean distance between rip channels was found to be 0.25 statute miles. The standard deviation of the distance between channels was found to be 0.09 miles for a ten mile section of beach along Clatsop Spit. These observations were made during a period of low waves.

BEACHES BORDERED BY IRREGULAR SUBMARINE TOPOGRAPHY

As yet there has been no quantitative approach to the prediction of currents or circulation along beaches bordered by irregular submarine topography. The situation differs from that existing along straight beaches with parallel contours in that the direction of longshore currents is dependent not only on the angle of wave approach but on the localized piling up of water on the beach at points of wave convergence. This local rise of sea level, the degree of which is still un-

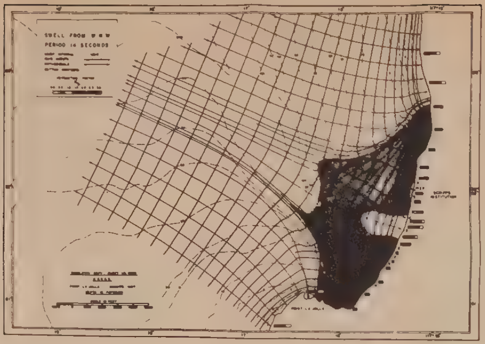

Fig. 5. Wave refraction diagram showing areas of wave convergence and divergence near La Jolla. The relative wave height is given by the length of the bar at various points along the beach. The letters A through H locate the same beach stations shown in Figs. 6 and 7. (From Munk and Traylor, 1947.)

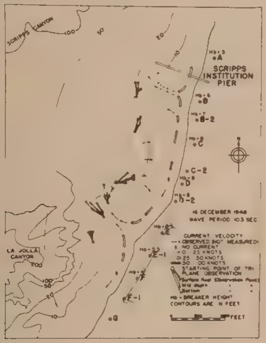
SCRIPPS CANYON
SCRIPPS INSTITUTION PIER
LA JOLLA CANYON
16 DECEMBER 1948
WAVE PERIOD 10.3 SEC
CURRENT VELOCITY
FEET

Fig. 6. The cell-like features of the nearshore circulation at Scripps Beach, La Jolla. The point of wave convergence is at station D, as shown by breaker height notation. (From Shepard and Inman, 1950.)

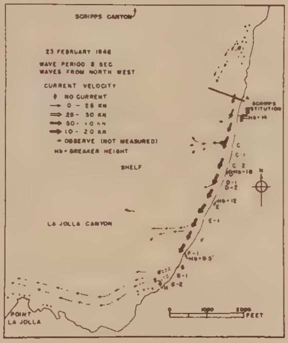
SCRIPPS CANYON
23 FEBRUARY 1948
WAVE PERIOD 8 SEC
WAVES FROM NORTH WEST
CURRENT VELOCITY
NO CURRENT
OBSERVE (NOT MEASURED)
HB = BREAKER HEIGHT
SHELF
LA JOLLA CANYON
SCRIPPS INSTITUTION
POINT LA JOLLA
FEET

Fig. 7. For short period waves the wave convergence is not as pronounced, and the direction of longshore current is controlled by the direction of wave approach. (From Shepard and Inman, 1950.)

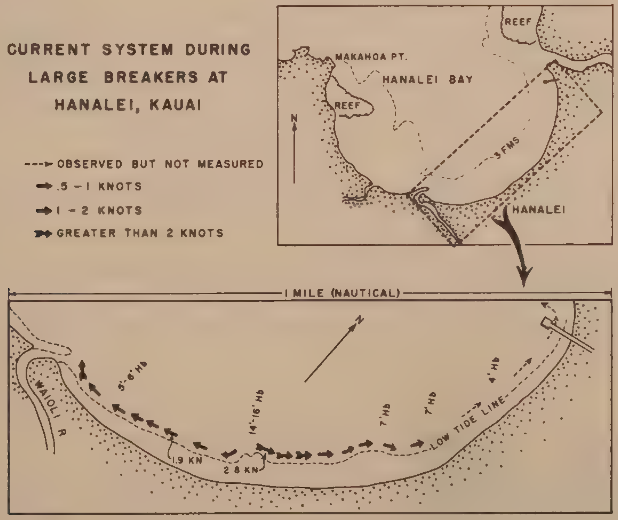
CURRENT SYSTEM DURING LARGE BREAKERS AT HANALEI, KAUAI
OBSERVED BUT NOT MEASURED
.5 – 1 KNOTS
1 – 2 KNOTS
GREATER THAN 2 KNOTS
REEF
MAKAHOA PT.
HANALEI BAY
REEF
N
3 FMS
HANALEI
1 MILE (NAUTICAL)
N
5'-6' Hb
14'-16' Hb
7' Hb
7' Hb
4' Hb
LOW TIDE LINE
WAIOLI R.
1.9 KN
2.8 KN

Fig. 8

known, results in a gradient along the beach and accompanying flow in both directions away from the convergence. These currents may be opposed in direction to the angle of wave approach.

Submarine canyons. Near those places where submarine canyon heads approach closely to the coast there are striking examples of wave convergence. At the canyon head the wave orthogonals diverge, decreasing the wave height, whereas they converge on either side, increasing the wave height (Fig. 5). In the La Jolla area it is not uncommon for the breaker height to be 10 times as high north of the two canyon heads as it is inside the heads. Current measurements outside the breakers at the convergence north of La Jolla Canyon indicate a movement towards the beach from the top to the bottom (Fig. 6). Inside the breakers the longshore currents flow away from the convergence in either direction. Rip currents commonly develop at points between the convergence and the divergence zone, where the waves are intermediate in height.

The current systems have been studied in two areas where canyon heads closely approach the coast: at La Jolla (Shepard and Inman, 1950) and at Mugu (Inman, 1950). In both areas the circulation pattern was found to be primarily dependent on the wave period. The longer period waves resulted in a sufficient degree of convergence so that the longshore currents flowed away from the zone of convergence. In this case the circulation cell is well developed and essentially fixed in position (Fig. 6) except as shifted slightly by changes in direction of wave approach. For shorter period waves the convergence is not as pronounced and the direction of wave approach becomes the controlling factor in determining the direction of longshore currents (Fig. 7). In this case the circulation cells are less stable and the position of the rips along the beach is variable. At La Jolla a strong blow accompanied by short period waves approaching diagonal to the coast produces constant current directions with the most pronounced rip at the bend in the coast in the down current direction (Fig. 7).

Crescentic Bay. On the north coast of Kauai in the Hawaiian Islands, Hanalei Bay forms a large crescentic bight into the main trend of the coast. During periods of high waves a large variation in wave heights was observed in a short distance along this bay (Fig. 8). In about a quarter of a mile breaker heights were observed to decrease from as much as 18 feet to 5 feet in one direction and at about half that rate in the other direction. This contrast is only partially explained by the small reefs which fringe both sides of the entrance. The highest breakers were comparable to those on the open coast so that they do not represent a convergence except relative to the adjacent portions of the bay. The longshore currents respond to this relative convergence in the same way as observed in areas adjacent to canyon heads. Currents as high as three knots were measured. At the point of greatest breaker height there is a low ridge extending seaward and the wave crests are bent around this ridge so that they come in directly against the strong outflowing currents. The flow is so strong as to produce a pronounced trough along the shore. In places these troughs are bordered by escarpments in the sand. As can be seen in Fig. 8, the flow away from the zone of high waves extends along the shore as much as three-quarters of a mile.

It is felt that these two cases including submarine canyons and crescentic bay by no means exhaust the possibilities of developing a local convergence with resulting divergent flow of longshore currents.

Small crescentic bays often show currents flowing in at one side and out on the other. During a 60 mile an hour gale at Nahant, Mass., currents were observed flowing in on one side of a small bay with velocities averaging about 4 or 5 knots. The outflow on the other side was much slower, indicating that there was a subsurface return flow. The surface inflow was continuous although considerably retarded during wave troughs.

CIRCULATION IN RELATION TO OBSTRUCTIONS

Points, breakwaters, and piers all influence the circulation pattern and alter the direction of the currents flowing along the shore. In general these obstructions determine the position of one side of the circulation cell. In places where relatively straight beaches are terminated on the down current side by points or other obstructions, a pronounced rip extends seaward. During periods of large waves having strong diagonal approach these rips can be traced seaward for one or more miles.

At the north jetty of the Mission Bay Breakwater a seaward flow was frequently observed in the current lee of the jetty. This same seaward flow north of the jetty exists under most other observed directions of wave approach (Fig. 9).

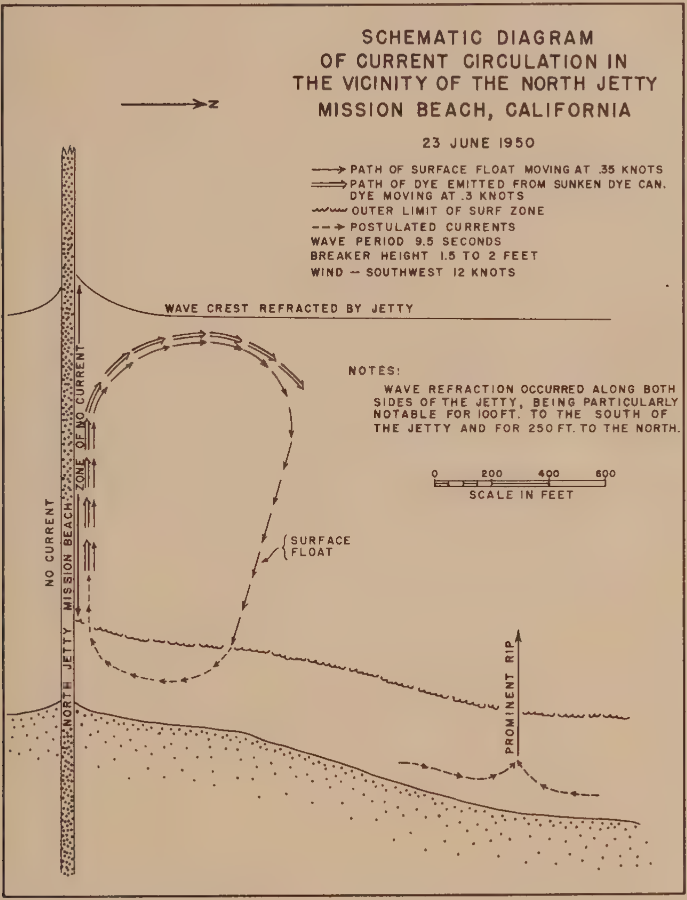
SCHEMATIC DIAGRAM
OF CURRENT CIRCULATION IN
THE VICINITY OF THE NORTH JETTY
MISSION BEACH, CALIFORNIA
23 JUNE 1950
N
PATH OF SURFACE FLOAT MOVING AT .35 KNOTS
PATH OF DYE EMITTED FROM SUNKEN DYE CAN. DYE MOVING AT .3 KNOTS
OUTER LIMIT OF SURF ZONE
POSTULATED CURRENTS
WAVE PERIOD 9.5 SECONDS
BREAKER HEIGHT 1.5 TO 2 FEET
WIND — SOUTHWEST 12 KNOTS
WAVE CREST REFRACTED BY JETTY
NOTES:
WAVE REFRACTION OCCURRED ALONG BOTH SIDES OF THE JETTY, BEING PARTICULARLY NOTABLE FOR 100 FT. TO THE SOUTH OF THE JETTY AND FOR 250 FT. TO THE NORTH.
0 200 400 600
SCALE IN FEET
SURFACE FLOAT
NO CURRENT
MISSION BEACH
NORTH JETTY
ZONE OF NO CURRENT
PROMINENT RIP

Fig. 9

Where prominent points of land interrupt the predominant longshore current flow, currents opposite in direction to that of the coast in general are likely to develop in the current lee of the point. Examples of this reverse flow have been observed in the lee of Dana Point (See Fig. 1 for location). Indirect evidence of currents flowing in this reversed direction are found where spits extend north in the current lee of obstructions such as at Morro Rock along the central California coast.

ACKNOWLEDGMENTS

The writers were assisted in field operations by Capt. W. H. Quinn, USAF, Lt. A. E. May, USN, Lt. Comdr. E. V. Mohl, USN, D. B. Sayner, Ruth Young, Comdr. R. Panzarini, Argentine Navy, J. D. Frautschy, H. R. Gould, Ruth Inman, R. L. Wisner, A. A. Allanson, and W. Jewell. Helpful suggestions in the course of the work came from W. H. Munk and R. S. Arthur.

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SAND MOVEMENT ON THE SHALLOW INTER-CANYON SHELF AT LA JOLLA, CALIFORNIA

TECHNICAL MEMORANDUM NO. 26
BEACH EROSION BOARD
CORPS OF ENGINEERS

NOVEMBER 1951

Contribution from the Scripps Institution of Oceanography, New Series, No. 533

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FOREWORD

This paper has been prepared by Dr. Francis P. Shepard and Douglas L. Inman in partial fulfillment of a contract between the Scripps Institution of Oceanography and the Beach Erosion Board for "research in connection with study of waves and currents in shallow ocean waters." The subject of the paper concerns more specifically Item 3 of the contract, which provides for "studies of the variation of beach profiles at and near Mission Beach, California, and elsewhere, with respect to wave and current conditions including analysis of the effects of submarine canyons and variability of beach and shore materials."

The report concerns 13 months of repetitive observations of a triangular shelf situated between the two main branches of La Jolla Submarine Canyon. The area selected is unique in that it affords an opportunity to gain at least qualitative information concerning the movement of littoral material past a submarine canyon and the losses of shore material which may occur by deposition in the canyon depths. The investigators have taken special care in an attempt to reduce the error of measurements taken in the course of the study.

This report is further identified as Scripps Contribution No. 533, and it appeared earlier as Submarine Geology Report No. 21. The data obtained are considered to be of sufficient value and general interest to merit publication at this time. The opinions and conclusions expressed by the authors are not necessarily those of the Beach Erosion Board.

SAND MOVEMENT ON THE SHALLOW INTER-CANYON SHELF AT LA JOLLA, CALIFORNIA

by

F. P. Shepard and D. L. Inman

ABSTRACT

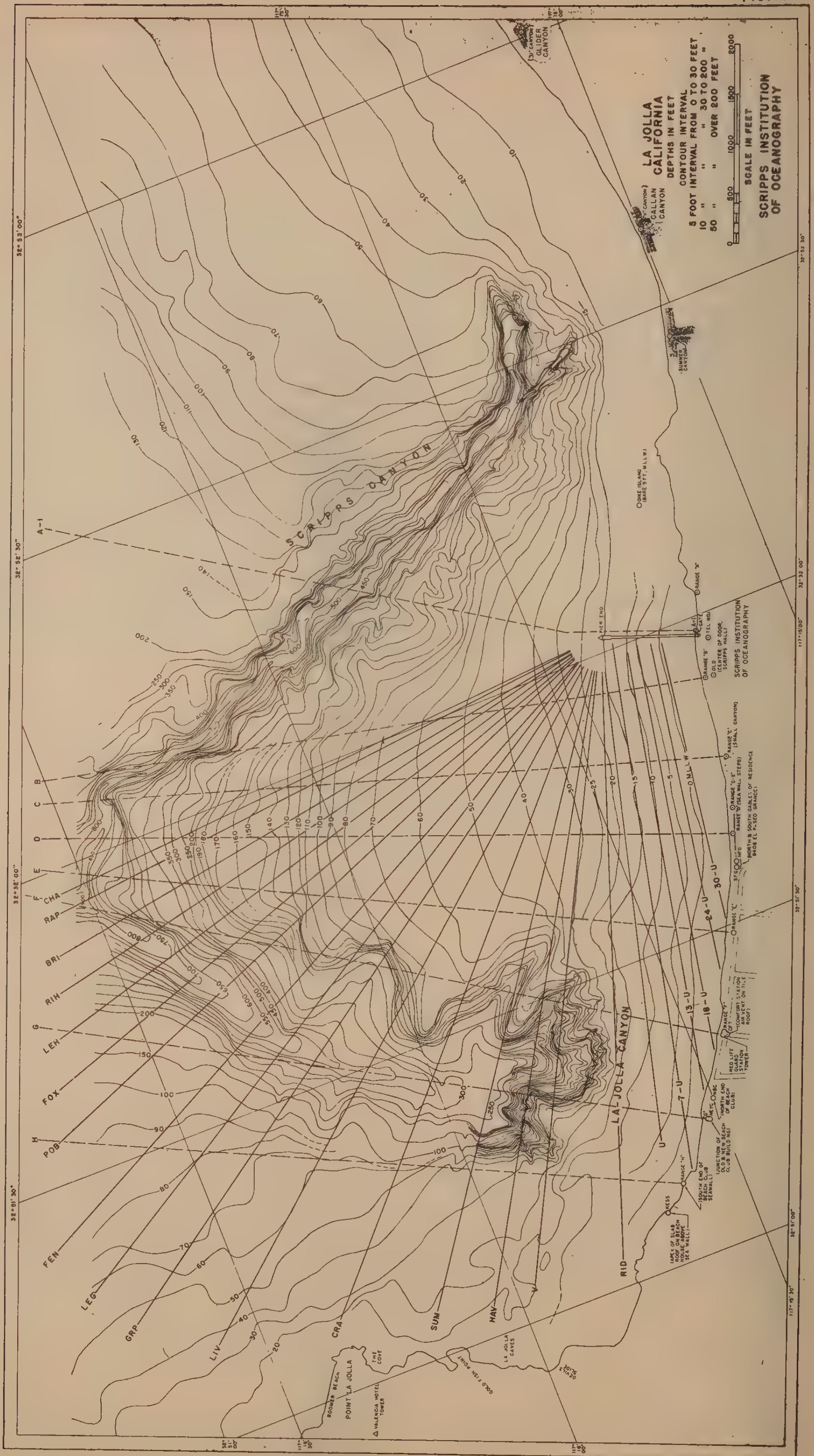
The nature of changes in sand level of a beach and shallow shelf area between two submarine canyon heads has been indicated by 8 repeated surveys accompanied by 5 sand sampling operations. It is believed that these surveys establish significant cut and fill out to depths of at least 100 feet. During large waves sediment is lost to the area by transportation into the submarine canyons. Replenishment of the sediment is apparently due to transport around the head of the northern of the two submarine canyons. The amount of sand introduced in this way is estimated to be of the order of 100 times as much as introduced from erosion of the land adjacent to the intercanyon area. On the other hand, little sand is carried around the southern canyon. Along and near the shore sand is moved seaward during large waves and landward during small waves. With diagonal approaching waves much sand is carried along the coast. On the outer shelf the movement takes place more parallel to the shore than normal to it. The accuracy of repeat surveys is discussed with suggestions as to the best methods.

Introduction

North of Point La Jolla the two main branches of La Jolla Canyon extend in to within about 700 feet of low tide shore line (Figure 1). Between these canyons there is a triangular shelf area with its apex a mile from shore and a base consisting of the relatively straight shore which runs for a mile and a half between the canyons. We had considered that this province, consisting of shelf and beach, might represent somewhat of an isolated area receiving little sediment from the outside due to the barriers represented by the canyons on each side and therefore that it might be of special interest in determining the seasonal shifts of sand which are known to accompany the seasonal changes in wave height, period and direction of approach.

The depth profiles across this triangular area and at the head of La Jolla Canyon were initiated in 1945, but the earlier work was not very satisfactory and did not extend seaward far enough to include the important zone beyond 50 feet in depth. Therefore, the present paper will be based largely on the results obtained between April 1949 and May 1950. During this period 8 complete bottom surveys were made. In addition to the sand level surveys, sampling of the bottom along the profiles on 5 occasions has provided information concerning the nature of sand movements. The

FIGURE 1


LA JOLLA
CALIFORNIA
DEPTHS IN FEET
CONTOUR INTERVAL
5 FOOT INTERVAL FROM 0 TO 30 FEET
10 " " 30 TO 200 "
50 " OVER 200 FEET
0
500
1000
1500
2000
SCALE IN FEET
SCRIPPS INSTITUTION
OF OCEANOGRAPHY
SCRIPPS CANYON
LA JOLLA CANYON
GLIDER CANYON
CALLAN CANYON
SUMNER CANYON
PIER END
SCRIPPS INSTITUTION OF OCEANOGRAPHY
POINT LA JOLLA
BOOMER BEACH
THE COVE
LA JOLLA CAVES
VALENCIA HOTEL TOWER
32° 53' 00"
32° 52' 30"
32° 52' 00"
32° 51' 30"
32° 51' 00"
117° 15' 00"
117° 15' 30"
117° 16' 00"
117° 16' 30"
A-1
B
C
D
E
F
G
H
CHA
RAP
BRI
RIH
LEH
FOX
POB
FEN
LEG
GRP
LIV
CRA
SUM
HAV
RID
U
7-U
13-U
18-U
24-U
30-U
0 MLLW
RANGE "A"
RANGE "B"
RANGE "C"
RANGE "H"
KRESS

results from this sediment study, however, will not be considered except briefly in the present report.

The surveys under discussion represent an extension of previous studies which have included hundreds of profiles along the 1,000-foot Scripps Institution pier (Shepard and LaFond, 1940), years of observation and measurement of the beach which extends along the shore for a mile south of Scripps Institution (Shepard, 1950), and observations of the nearshore circulation in the waters adjacent to the beach (Shepard and Inman, 1950). The shelf and beach profiles are also related to the depth changes in the canyon heads of this area which have been observed for many years (Shepard, 1951).

Methods and Accuracy of the Surveys

The accuracy of a marine survey is in general of a far lower order than is that of a land survey. This has been recognized by the U. S. Coast and Geodetic Survey so that despite the fact that they have had an outstanding group of surveyors and have used very precise methods, they have been very cautious in claiming that their surveys demonstrate depth changes other than those in harbors and those involving the shifting of bars near the entrances to bays. This reluctance has been partly because little attempt has been made to repeat surveys along predeveloped ranges. The Army Engineers and various city and state organizations, however, have made repeated surveys along predeveloped ranges which provide a much better opportunity for comparison.

The method employed by the Beach Erosion Board which involves the use of Amphibious Vehicles (Dukws) equipped with large-scale echo sounding devices and shore position control by transit telescopes and three-way radio communication is certainly an excellent system but like every other system so far devised is subject to uncertainty, particularly in the outer portions of lines. It is in these portions that some large apparent changes have been reported.

The surveys made by the group at Scripps Institution, also using a Dukw, have included methods which were in some respects inferior to those employed by the Beach Erosion Board, but we have tried to make up for the deficiencies by using a double check method. We have run our lines along ranges consisting of relatively permanent shore points (Figure 1). At short intervals, cross ranges have been used as fixes for marking the echo sounding tape.[1] In order to check each of these positions, sextant angles have been read coincident with the passing of the cross range. Also, a shore group have been using a transit telescope and have signalled the Dukw when it was off range. By using these methods of checks we have found that all cases where large changes were indicated in the outer portions of the surveys were explainable by position errors. Another check which we have used to some extent is the rerunning of the surveys

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1/ Not all of the cross ranges are shown on Figure 1 because of crowding of the lines near shore.

particularly in the outer portion where inaccuracies are most likely. These rerun surveys increase the degree of confidence in the methods. So far as we know these repeat runs have rarely been made by surveyors in order to check the accuracy of their methods.

In coastal engineering practice it is customary to check echo soundings against wire soundings in shallow water. A system which we have employed to some extent is to check the accuracy of the echo sounding device by vertical casts at a variety of depths including the outer portions of the lines (that is, except where the slopes are so steep as to make necessary a considerable slope correction). In general we have found little need to apply depth corrections on the fathogram other than tidal and have no good indication of depth changes of appreciable size (that is, of as much as 1 foot) as the result of temperature gradients.

In running a survey line in to shore and up onto the beach there is a zone where the breakers are traversed and hence where echo soundings are difficult, if not impossible. When there are small breakers, however, the gap between the termination of echo soundings and the position where the Dukw touches bottom is very slight. As a result, we have found that we could obtain a fairly accurate profile by starting land controlled surveys with a transit rod located on the front of the Dukw as soon as the Dukw wheels were resting firmly on the bottom. During this inner traverse the party on the Dukw signal to the shore party when the Dukw is on each of the closely-spaced cross ranges (each pier piling on a distant object). It is our feeling that this method of traversing the breakers is superior to lead line soundings in this difficult zone. An easy test of the relative merits of the two could be obtained by double runs with both methods.

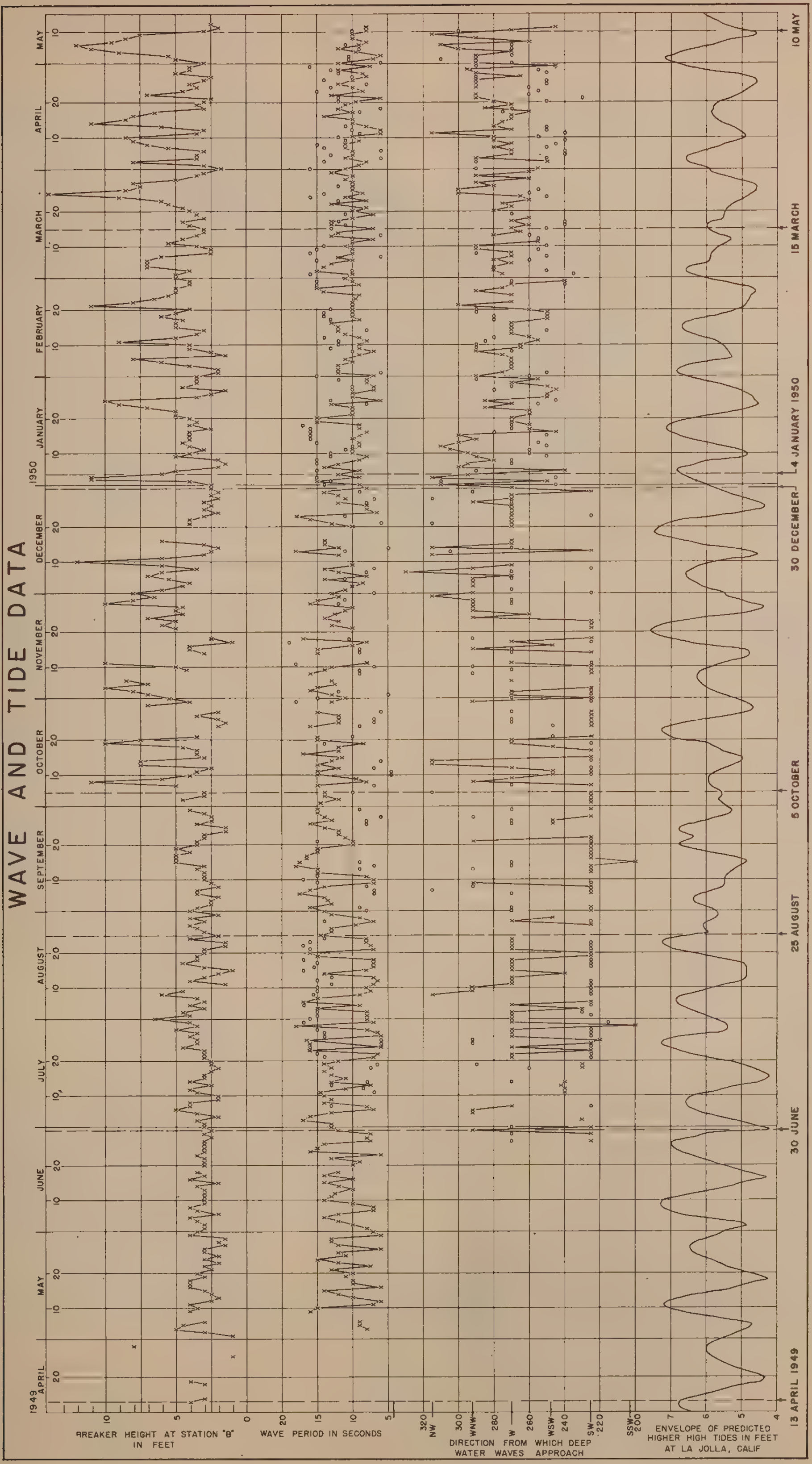
On additional advantage which the surveys at Scripps Institution may have had on some others is that the surveys have been conducted by those who were scientifically interested in the formation which the surveys produced. In evaluating the results of any survey one should not overlook this personal equation. It seems to us that whereever possible the scientists who are going to use the data should participate in the surveys.

Waves

Daily wave height, period, and deep water direction were observed throughout the time of the surveys with the exception of the period from 13 April to 30 June, 1949, when only wave height and period were observed. These data are shown graphically by days in Figure 2. The data tabulated in this figure are a compilation of information from several sources, the primary sources being:

a. Daily observations of breaker height, period, and general deep water direction at beach Station "B" and from Scripps Pier.

FIGURE 2



WAVE AND TIDE DATA

b. Observations of period and deep water directions from the 300-foot high cliff one half mile north of Scripps Institution.

c. Observations during 1950 by the Beach Erosion Board at Mission Beach, 5 miles south of La Jolla, (Forrest, 1951).

These data were supplemented by:

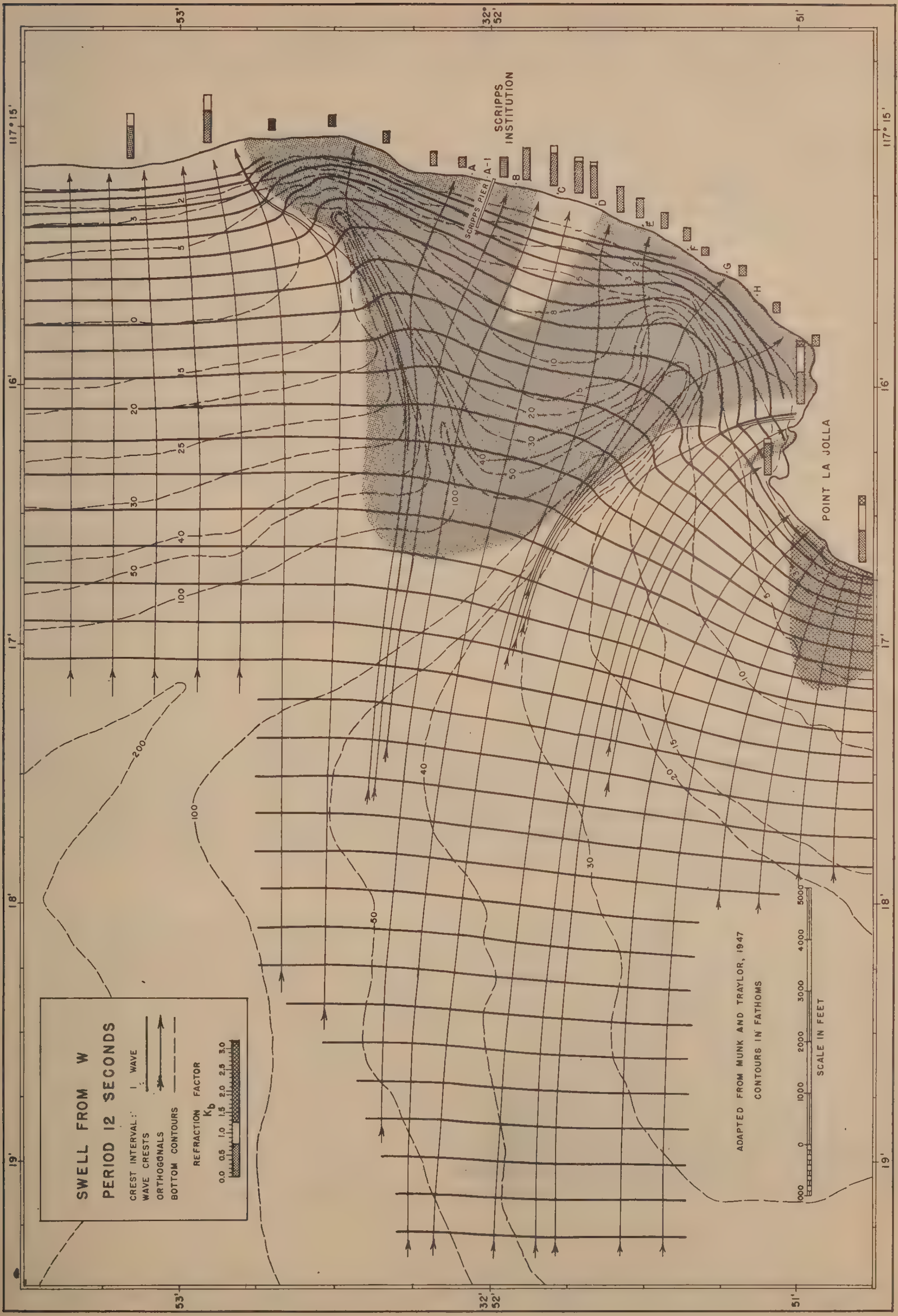
a. Observations of southern swell at Oceanside, California, (Wiegel and Kimberley, 1950).

b. Miscellaneous spot observations, such as by analysis of Scripps Institution wave meters, etc.

Recording of wave data was complicated by the fact that the breaker height was usually the result of two or more wave trains from different directions. If two trains of waves existed on a given day, they were recorded as major and minor trains (Figure 2 and 6). No attempt was made to record more than two wave trains, although more probably existed on many days. The direction of deep water wave approach is subject to much greater error than the wave period and height observations. The directions were recorded to within plus or minus 10 degrees, with the greatest accuracy being obtained for waves approaching from westerly and northwesterly directions. The exact direction of approach for southerly waves was very difficult to ascertain.

It seemed impractical to attempt to determine the individual deep water wave heights of each of the several wave trains that may have contributed to the breaker height of the significant waves. For this reason the wave height shown in all figures is the breaker height of the significant waves (average of the heights of the higher 1/3 of the breakers) observed at beach Station "B" during the day. The height of the breaking wave was determined by obtaining a line of sight from a graduated range pole (placed approximately at mean water level) to the wave crest and the horizon. The height of breaker was corrected to include the depth of the wave trough below mean water level by multiplying the range pole reading by 4/3 (Hydrographic Office, 1944, p. 27).

The height of the breakers, particularly for long period waves, is markedly influenced along Scripps Beach by wave refraction over the complex submarine canyon ridge topography in this area. The refraction usually results in a relative convergence and high waves near Station C and D, and divergence and lower waves to the north and south of these points (See Figure 3). To aid in interpreting the breaker height at Station "B" in terms of the remainder of the area, a wave refraction rose showing the breaker refraction factor K_b, for various wave periods and deep water directions of approach is given in Figure 4. The breaker refraction factor K_b gives the height of the breaking wave at Station "B" relative to the height of breaker that would result from an unrefracted wave of the same period and deep water height (Munk and Traylor, 1947).


SWELL FROM W
PERIOD 12 SECONDS
CREST INTERVAL: 1 WAVE
WAVE CRESTS
ORTHOGONALS
BOTTOM CONTOURS
REFRACTION FACTOR
K_b
0.0 0.5 1.0 1.5 2.0 2.5 3.0
ADAPTED FROM MUNK AND TRAYLOR, 1947
CONTOURS IN FATHOMS
SCALE IN FEET
1000 0 1000 2000 3000 4000 5000
SCRIPPS INSTITUTION
SCRIPPS PIER
A
A-1
B
C
D
E
F
G
H
POINT LA JOLLA
117° 15'
16'
17'
18'
19'
53'
32° 52'
51'
2
3
5
10
15
20
25
30
40
50
100
200

A wave refraction diagram for waves with a period of 12 seconds approaching from a deep water direction of 270 degrees (west) is given in Figure 3. Refraction diagrams for other periods and directions of approach are given by Munk and Traylor (1947).

Figures 5 and 6 present a summary of the character of the waves occurring between each survey. Figure 5 shows histograms of wave heights for each period, and Figure 6 shows the relation between breaker height, wave period and deep water direction of approach for both major and minor trains during the same periods.[2]

Inspection of these two figures shows that the summer and winter wave conditions are quite different. The waves during the summer (30 June to 5 October, 1949) have a mean breaker height at Station "B" of approximately 3 feet, and may be characterized by two predominant wave types: (a) waves with periods of 7 to 9 seconds approaching from a westerly direction, and (b) waves with periods of 13 to 17 seconds approaching from a southerly direction. These two types occurred with approximately equal abundance during the earlier part of the summer (30 June to 24 August 1949), with the latter becoming more abundant during the late summer (25 August to 4 October 1949).

The fall, winter and spring waves (5 October 1949 to 10 May 1950) show a much greater scatter in wave height, period, and direction of approach. The mean winter breaker height was higher than were the summer breakers, averaging about 5 feet, and there was a greater abundance of waves from a northwesterly direction.

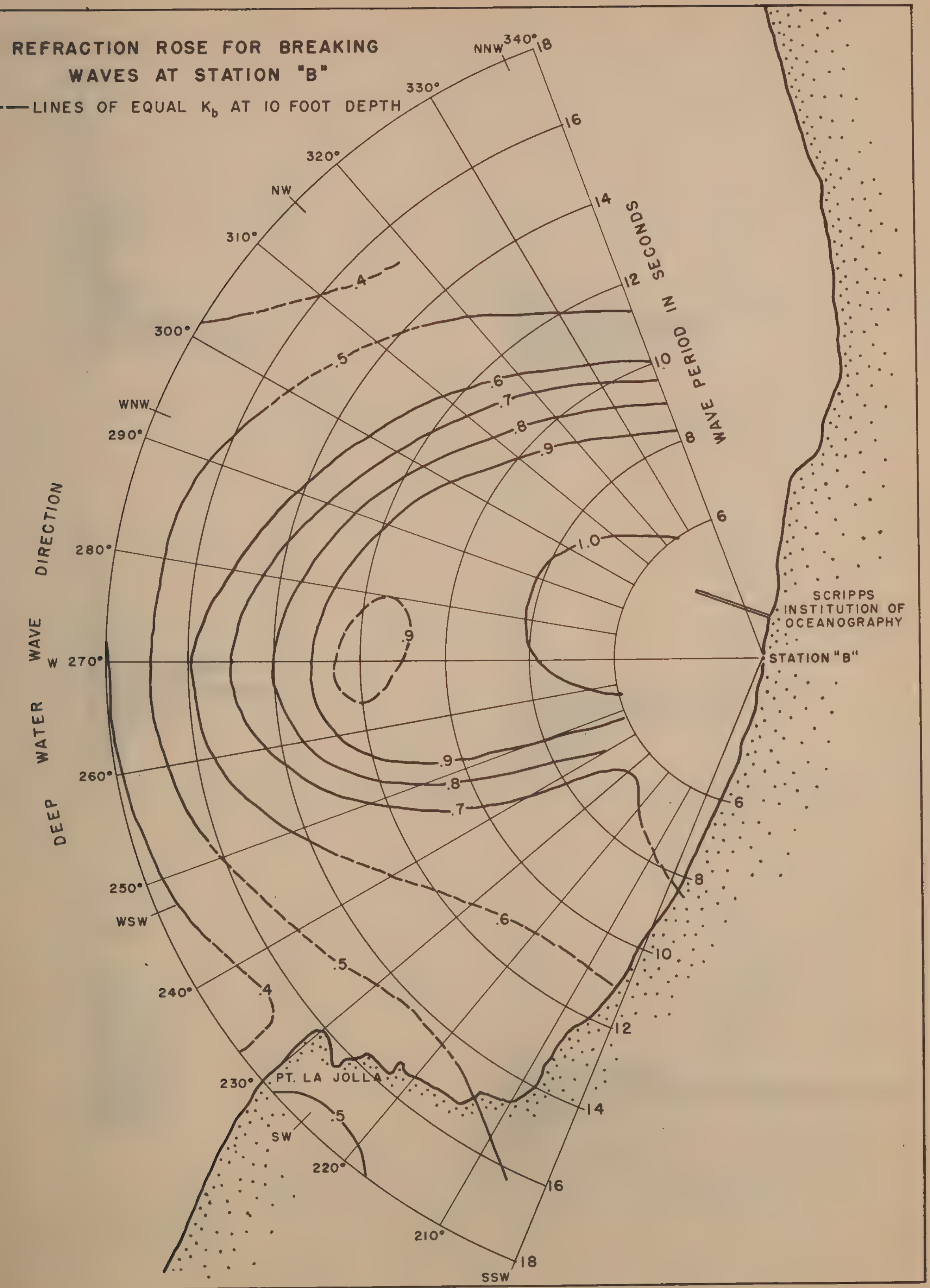
Sediments

Between June 1949 and May 1950 five series of beach and offshore sediment samples were obtained on dates as close as practical to the dates of the sand level surveys. Each series was taken on a grid corresponding to the survey ranges and cross ranges and consisted of about 130 samples extending from the beach foreshore out to depths of approximately 150 feet. In addition both beach and bottom samples were obtained to the north and south of this grid.

The greatest change in the size of the sediments occurred from the beach foreshore out to depths of 10 feet below mean lower low water. In depths greater than 20 or 30 feet there was very little change in the size of the bottom sediments with time. The sediments in depths less than 10 feet (including the beach foreshore samples) all fall within the Wentworth Grade of fine sand. The average median diameter for these sediments over the period of the surveys was .18 mm., with extreme ranges from .12 to .25 mm. The coarsest material was usually found in the surf zone at depths of 0 to 10 feet below M.L.L.W. (see Figure 7). In general, the median diameter of the bottom sediments decreases with increasing depth beyond the surf zone. The average median diameter in depths of 15 to 30 feet was .125 mm., and from 30 to 100-feet depth the average median was .10 mm.

2/ In Figure 6 both the major and minor wave trains are plotted as having the breaker height of the significant waves for the day. Thus the total number of days observed is the sum of the major train notations.

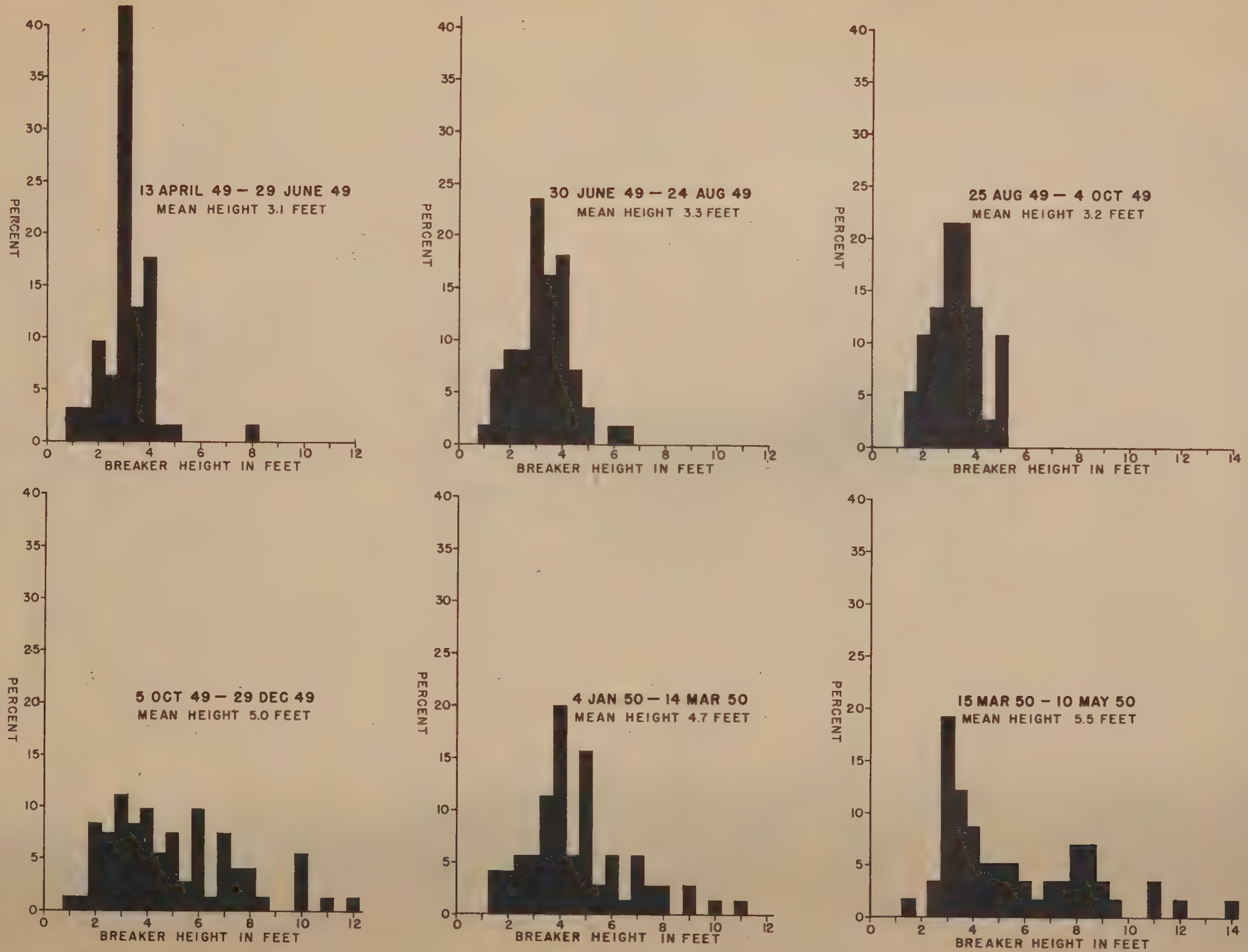
FIGURE 4



REFRACTION ROSE FOR BREAKING WAVES AT STATION "B"

— — LINES OF EQUAL K_b AT 10 FOOT DEPTH

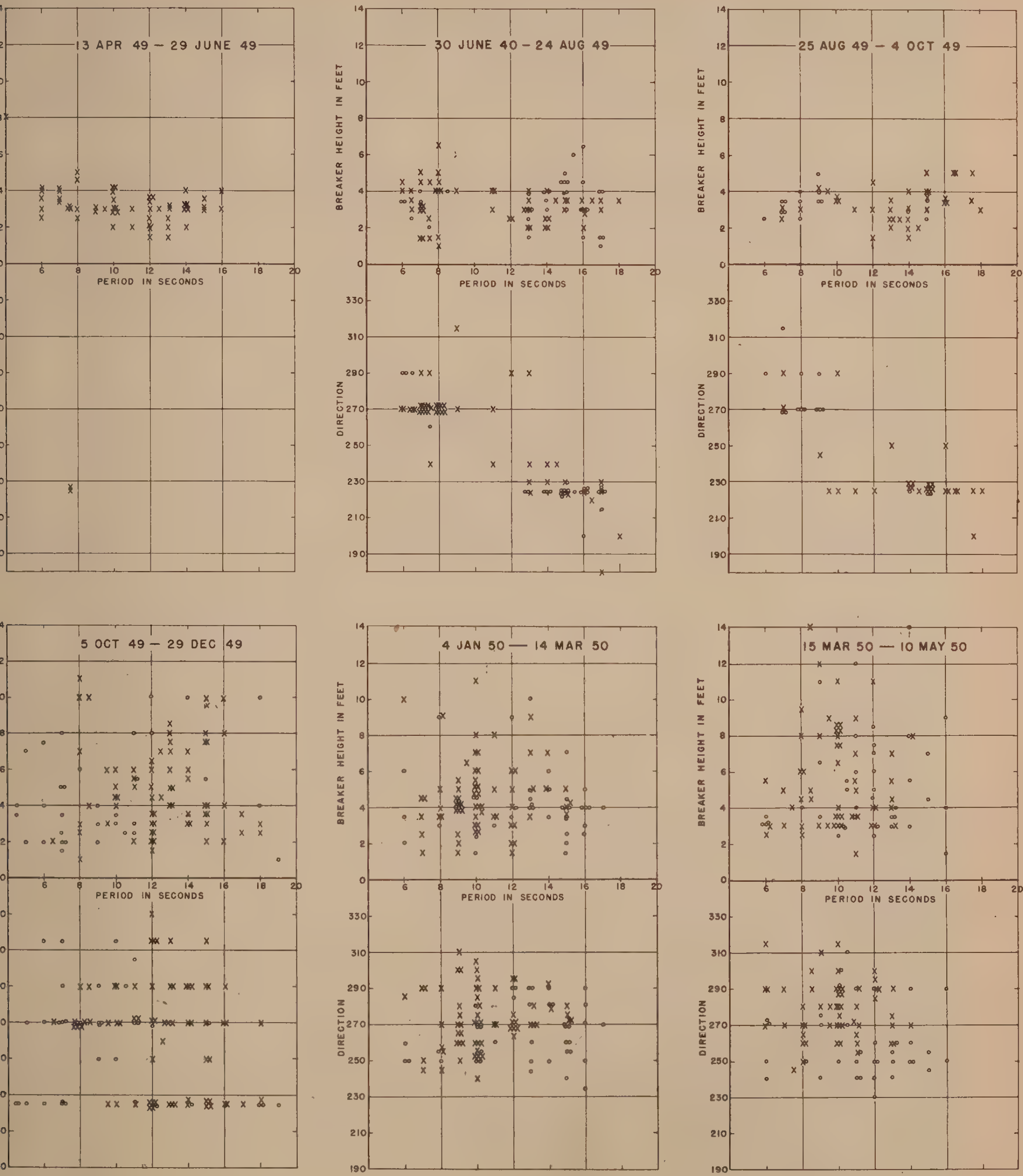
FIGURE 5



HISTOGRAMS OF BREAKER HEIGHT AT STATION "B"

MEAN BREAKER HEIGHT FOR ENTIRE PERIOD 4.2 FEET

FIGURE 6



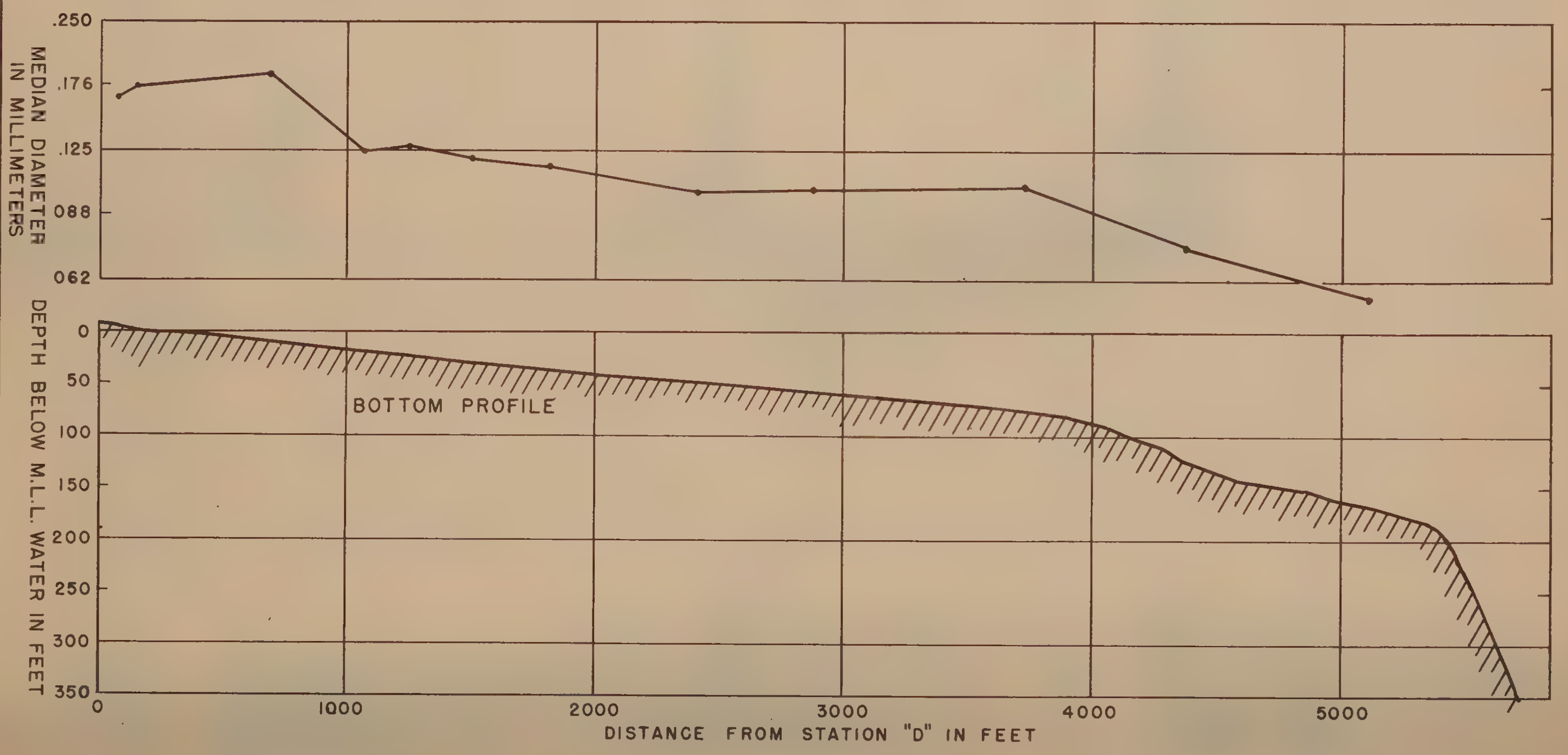
RELATION OF WAVE PARAMETERS

DIAGRAMS SHOW RELATION BETWEEN BREAKER HEIGHT AT STATION "B", WAVE PERIOD, AND DIRECTION FROM WHICH DEEP WATER WAVES APPROACH THE AREA. DAILY MAJOR WAVE TRAINS ARE INDICATED BY "X", MINOR TRAINS BY "O".

FIGURE 7

DISTRIBUTION OF SEDIMENT SIZE ALONG RANGE "D"

9 — 11 MAY 1950



The beach sediments are coarsest during the winter and spring when the beaches are cut back, and finer in the fall following the summer fill. During the August survey several large patches of cobbles were observed on "G" Range between depths of 5 and 10 feet.[3] The isopleth maps for this period show a cut of several feet in this region, and an accretion of the beach foreshore.

The sand along the beach for five miles north of Scripps Canyon head is very similar to the sand south of Scripps Institution. On the other hand, a much coarser sand is found on the south side of La Jolla Canyon, suggesting that there is relatively little sand exchange between the two sides of the canyon.

Observed Depth Changes

The diagrams (Figures 8 to 14) indicate the changes in sand level estimated as a result of the 8 surveys during the period between 13 April 1949 and 10 May 1950. These changes are in the form of isopleth maps, which give lines of equal cut or fill from one survey to the next. As indicated in the introduction, the surveys are subject to some inaccuracies and in addition much interpretation is necessary between the lines of the surveys. Nevertheless, the nature of the changes shows such a relationship to the observed wave conditions (Figures 2-6) that there seems little doubt about their qualitative value.

In considering the changes it seemed advisable to divide the area into a zone above and a zone below the 10-foot isobath (datum mean lower low water) as determined by a survey made at an earlier date. This division was based on the indication of some pivotal action at this depth in the present surveys and also on profiles of maximum annual cut and maximum annual fill along the Scripps Institution pier (Shepard, 1950, Figure 15). In figuring the total volume of change a planimeter was used to obtain the area between contours and estimates were made of the average change within the contours rather than taking the mean depth represented by the two contours. The net cumulative changes in the volume of sand in the nearshore, the offshore, and the total area are shown graphically for each survey period in Figure 15. The total area covered by the survey was 1,808,000 square yards, while the inshore area (depths less than 10 feet below mean lower low water) constituted 530,000 square yards, and the offshore area 1.278,000 square yards. In comparing the total net changes given in Figure 15 it should be observed that a net error of 0.1 foot in depth in the offshore survey will result in a net error of 43,000 cubic yards of material for this area. Although this places some limit on the interpretation of net changes, the individual changes are so much larger than 0.1 foot that they are less affected. Also the inshore surveys are

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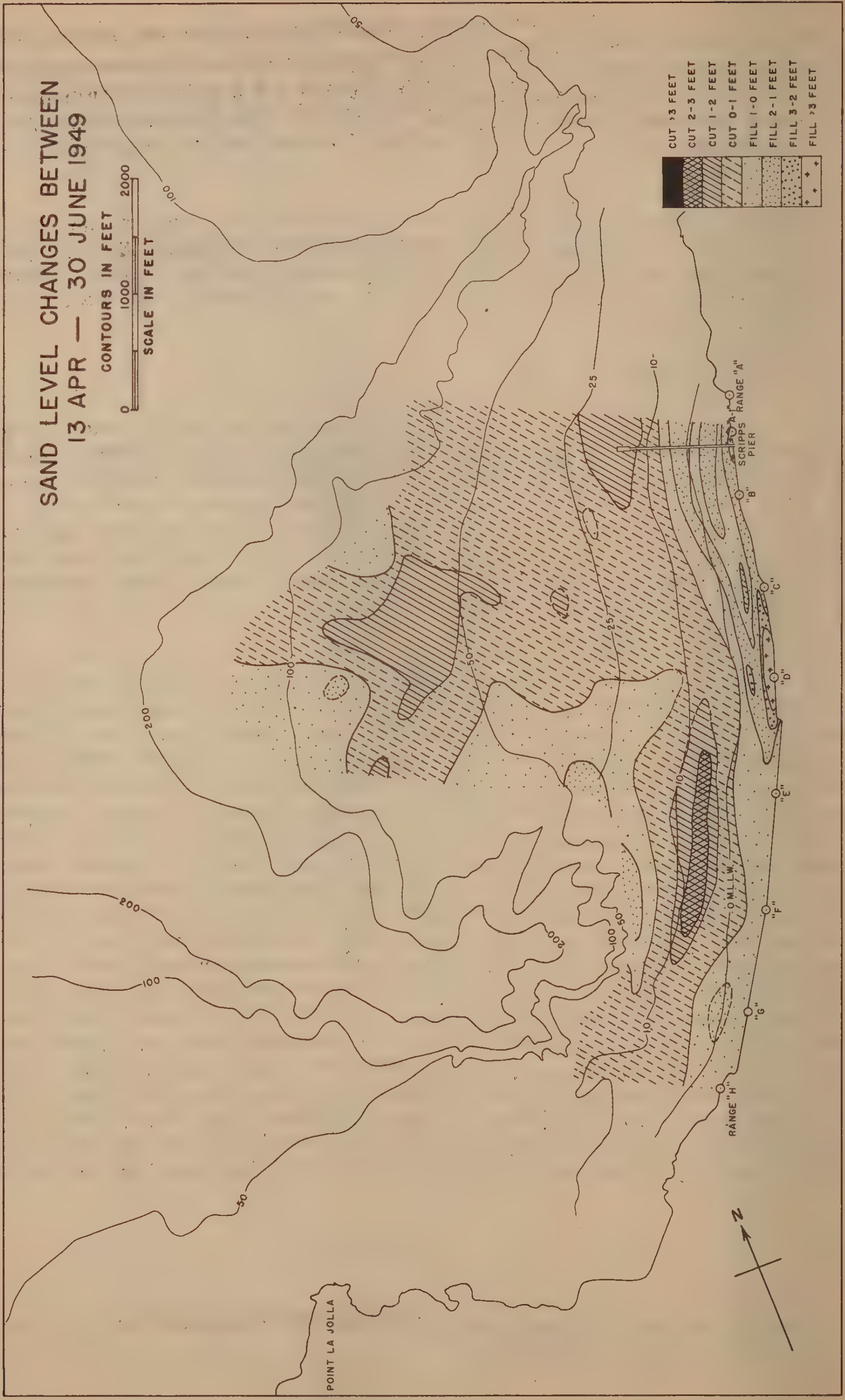
3/ In summers during the past, these cobbles have appeared as far inshore as the low tide shore line.

FIGURE 8

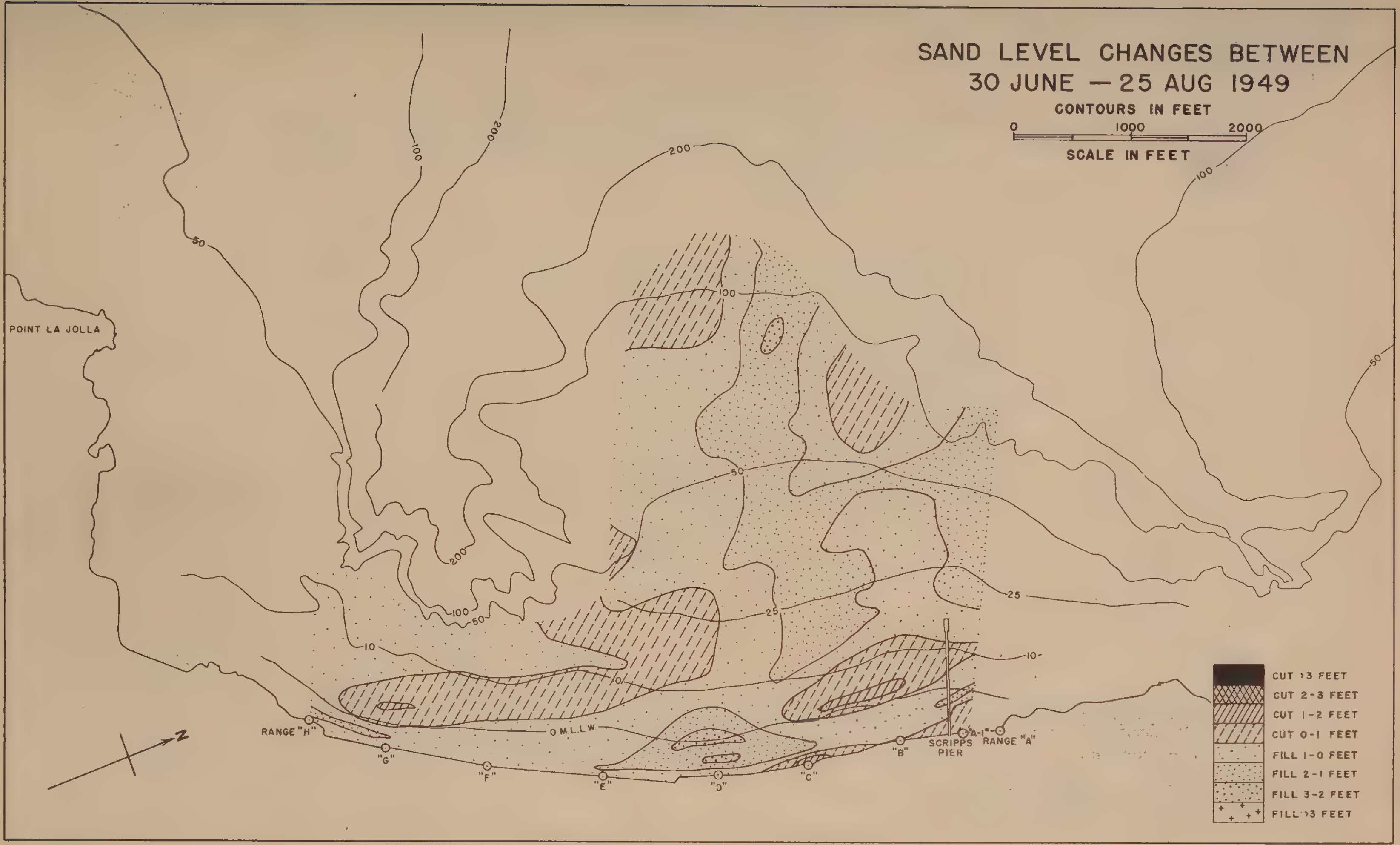


SAND LEVEL CHANGES BETWEEN 13 APR — 30 JUNE 1949

CONTOURS IN FEET

0
1000
2000
SCALE IN FEET
CUT >3 FEET
CUT 2-3 FEET
CUT 1-2 FEET
CUT 0-1 FEET
FILL 1-0 FEET
FILL 2-1 FEET
FILL 3-2 FEET
FILL >3 FEET
RANGE "A"
"A-1"
SCRIPPS PIER
"B"
"C"
"D"
"E"
"F"
"G"
RANGE "H"
0 M.L.L.W.
10
25
50
100
200
POINT LA JOLLA
N

FIGURE 9

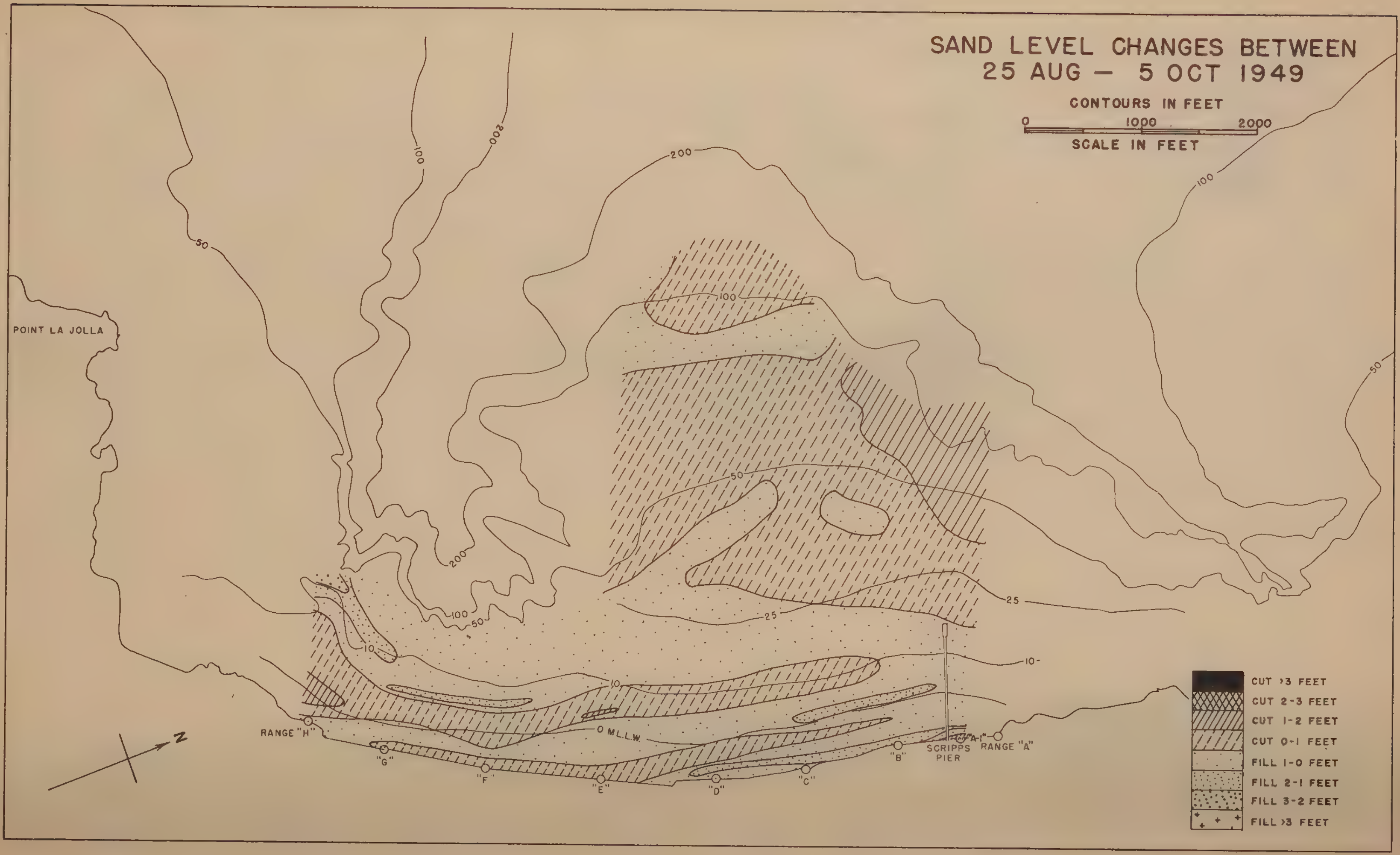


SAND LEVEL CHANGES BETWEEN 30 JUNE — 25 AUG 1949

CONTOURS IN FEET

0
1000
2000
SCALE IN FEET
CUT >3 FEET
CUT 2-3 FEET
CUT 1-2 FEET
CUT 0-1 FEET
FILL 1-0 FEET
FILL 2-1 FEET
FILL 3-2 FEET
FILL >3 FEET
POINT LA JOLLA
RANGE "H"
"G"
"F"
"E"
"D"
"C"
"B"
SCRIPPS PIER
A-1
RANGE "A"
0 M.L.L.W.
10
25
50
100
200
N

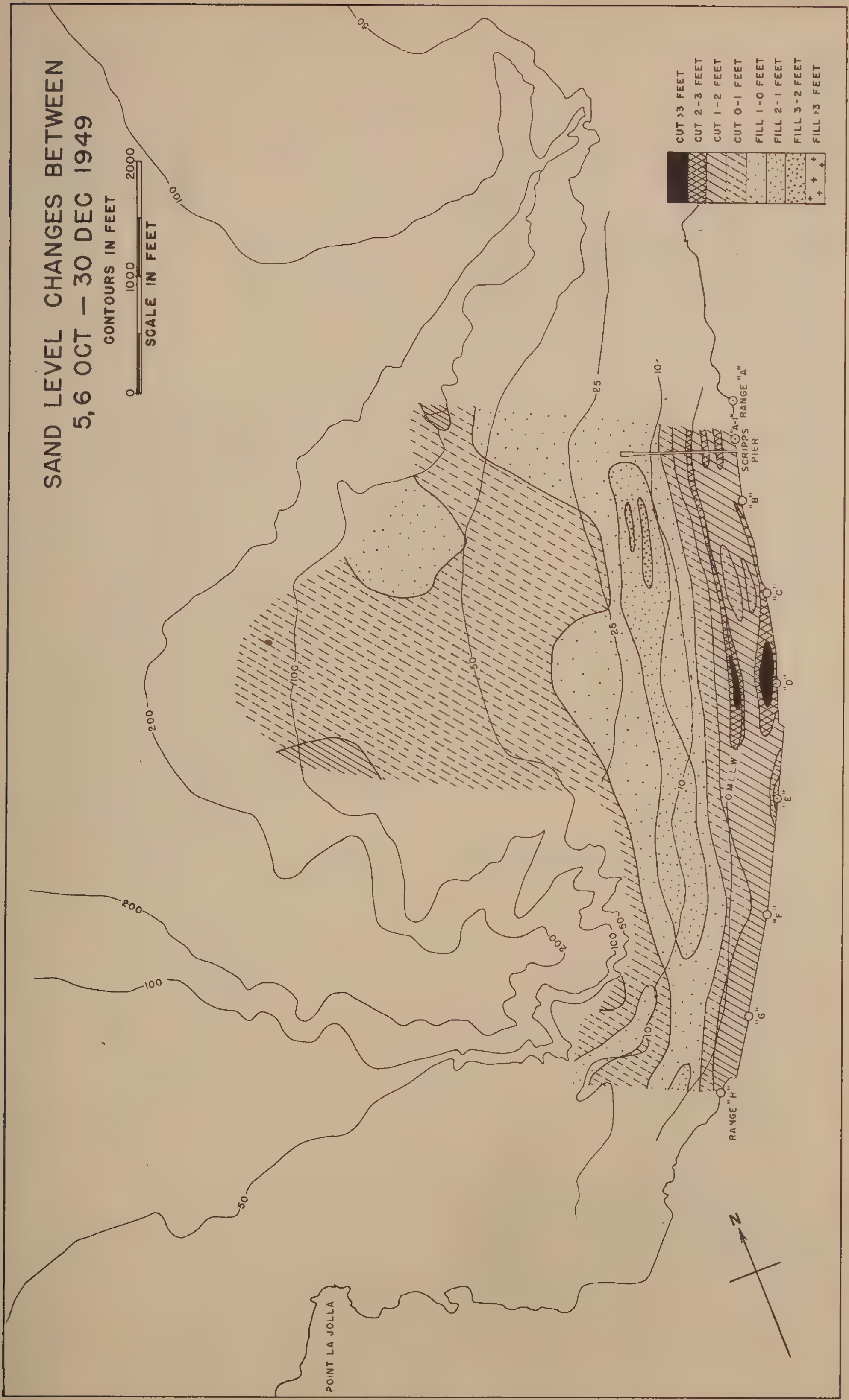
FIGURE 10



SAND LEVEL CHANGES BETWEEN 25 AUG — 5 OCT 1949

CONTOURS IN FEET
0
1000
2000
SCALE IN FEET
POINT LA JOLLA
RANGE "H"
"G"
"F"
"E"
"D"
"C"
"B"
"A-I"
RANGE "A"
SCRIPPS PIER
0 M.L.L.W.
10
25
50
100
200
N
CUT >3 FEET
CUT 2-3 FEET
CUT 1-2 FEET
CUT 0-1 FEET
FILL 1-0 FEET
FILL 2-1 FEET
FILL 3-2 FEET
FILL >3 FEET

FIGURE 11

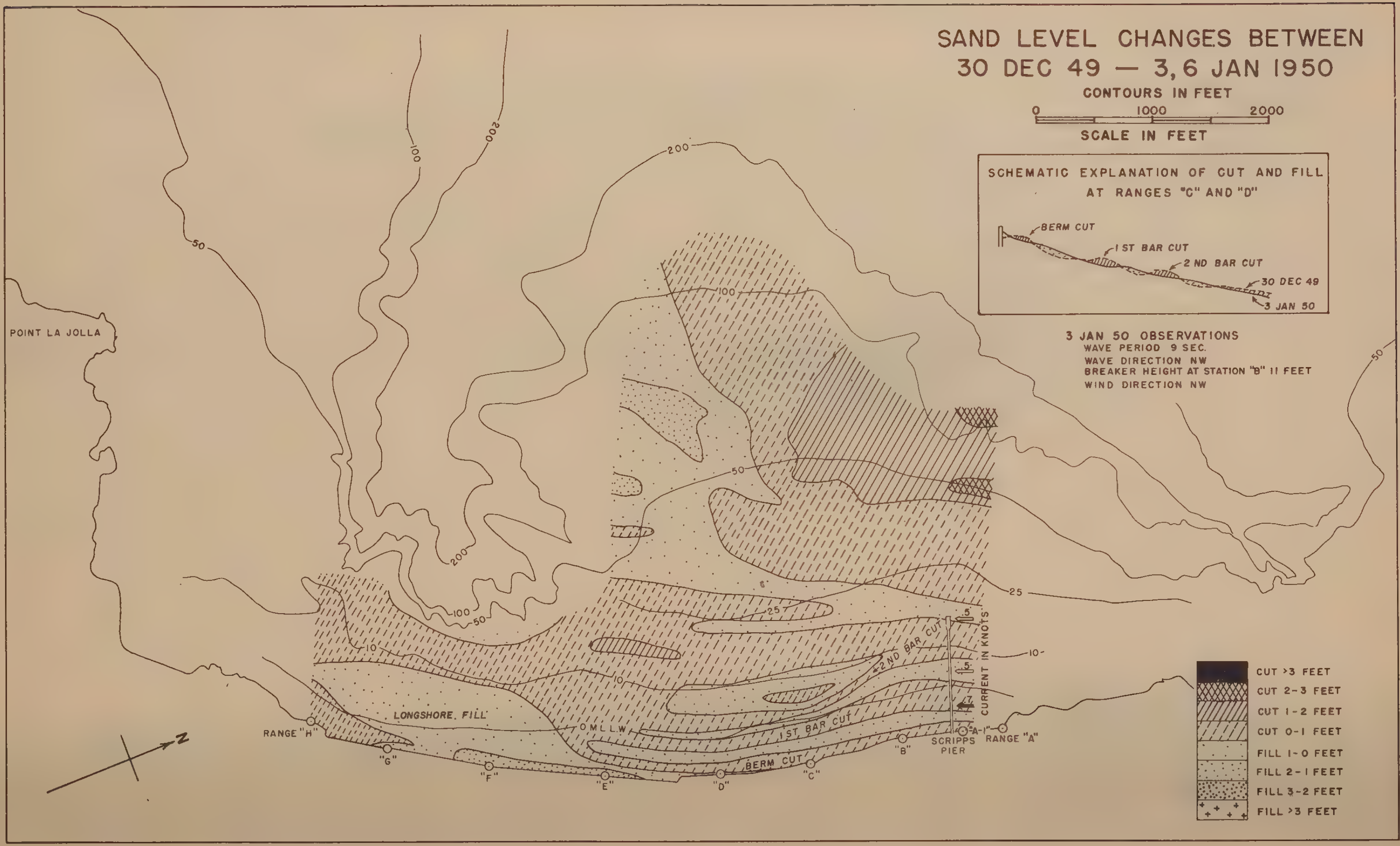


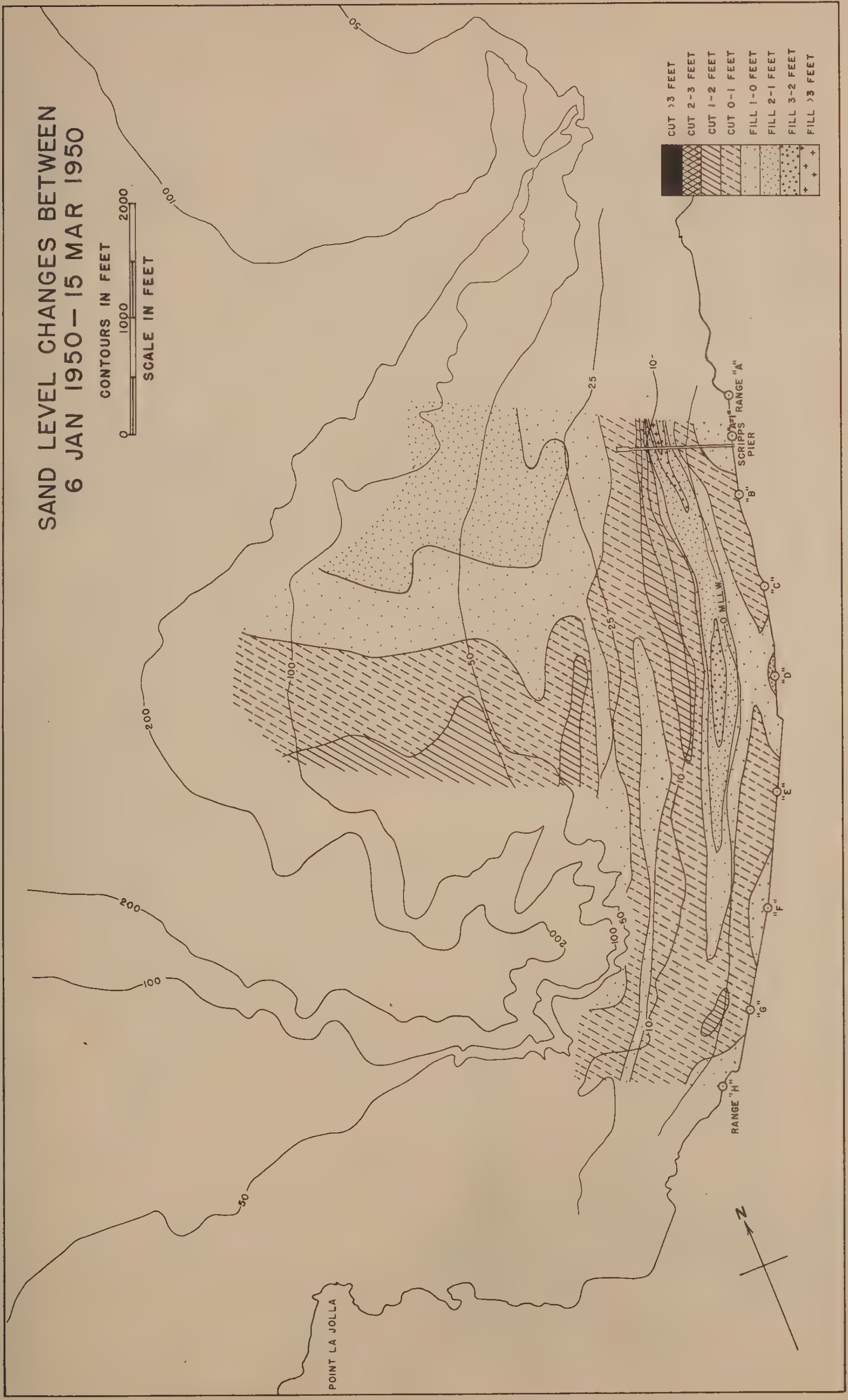
SAND LEVEL CHANGES BETWEEN 5,6 OCT — 30 DEC 1949

CONTOURS IN FEET

0
1000
2000
SCALE IN FEET
CUT >3 FEET
CUT 2-3 FEET
CUT 1-2 FEET
CUT 0-1 FEET
FILL 1-0 FEET
FILL 2-1 FEET
FILL 3-2 FEET
FILL >3 FEET
50
100
200
25
10
0 M.L.L.W.
RANGE "A"
"A-1"
SCRIPPS PIER
"B"
"C"
"D"
"E"
"F"
"G"
RANGE "H"
POINT LA JOLLA
N

FIGURE 12


SAND LEVEL CHANGES BETWEEN
30 DEC 49 — 3,6 JAN 1950
CONTOURS IN FEET
0
1000
2000
SCALE IN FEET
SCHEMATIC EXPLANATION OF CUT AND FILL AT RANGES "C" AND "D"
BERM CUT
1 ST BAR CUT
2 ND BAR CUT
30 DEC 49
3 JAN 50
3 JAN 50 OBSERVATIONS
WAVE PERIOD 9 SEC.
WAVE DIRECTION NW
BREAKER HEIGHT AT STATION "B" 11 FEET
WIND DIRECTION NW
POINT LA JOLLA
50
100
200
25
10
LONGSHORE. FILL
O M L L W
1ST BAR CUT
2 ND BAR CUT
BERM CUT
CURRENT IN KNOTS
.5
.7
RANGE "H"
"G"
"F"
"E"
"D"
"C"
"B"
SCRIPPS PIER
"A-1"
RANGE "A"
N
CUT >3 FEET
CUT 2-3 FEET
CUT 1-2 FEET
CUT 0-1 FEET
FILL 1-0 FEET
FILL 2-1 FEET
FILL 3-2 FEET
FILL >3 FEET

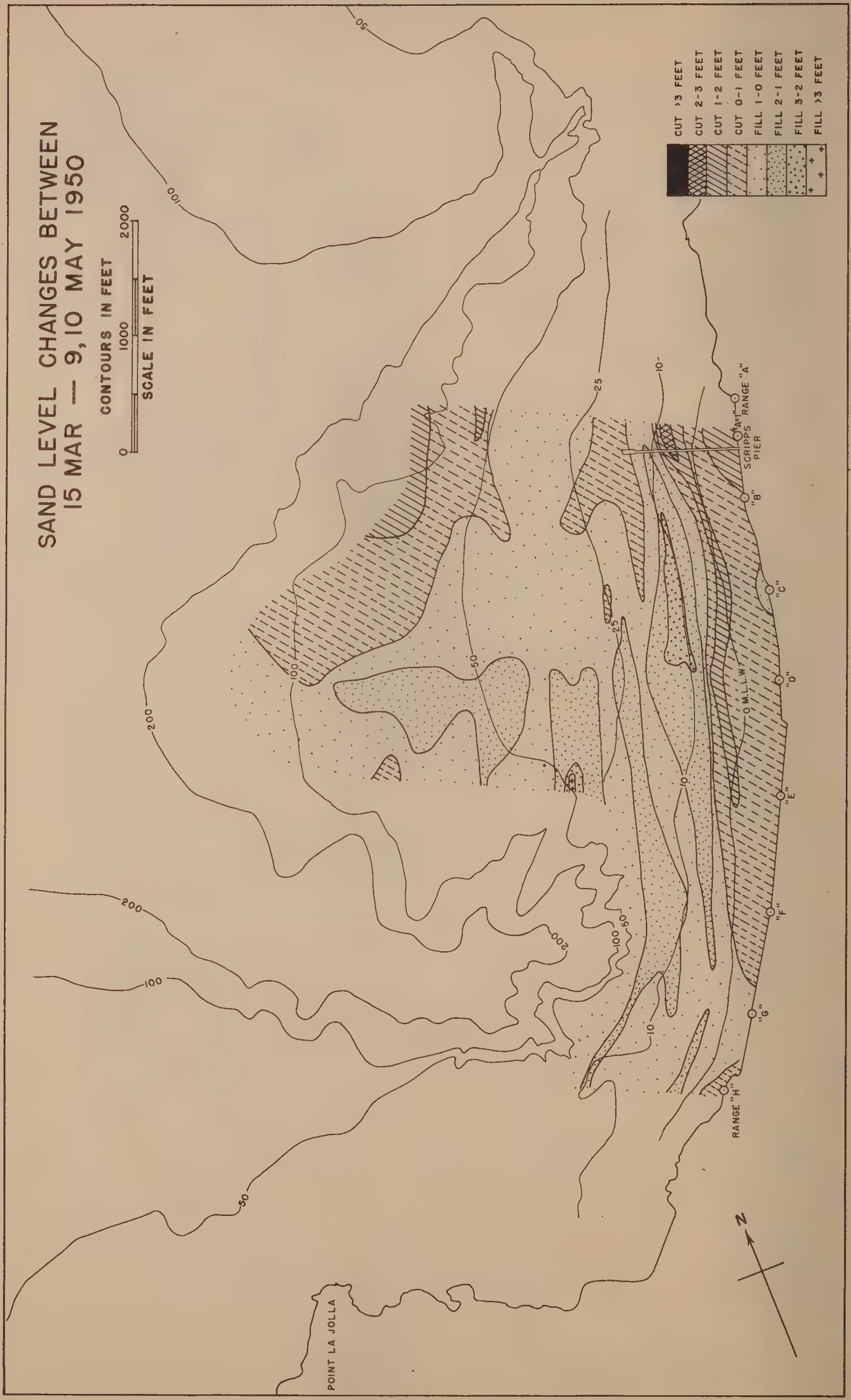


SAND LEVEL CHANGES BETWEEN
6 JAN 1950 – 15 MAR 1950

CONTOURS IN FEET

0
1000
2000
SCALE IN FEET
■ CUT >3 FEET
▩ CUT 2-3 FEET
▨ CUT 1-2 FEET
▨ CUT 0-1 FEET
· FILL 1-0 FEET
⁘ FILL 2-1 FEET
⁙ FILL 3-2 FEET
+ FILL >3 FEET
50
100
200
25
10
0 MLLW
SCRIPPS PIER
RANGE "A"
"A"
"B"
"C"
"D"
"E"
"F"
"G"
RANGE "H"
N
POINT LA JOLLA

FIGURE 14

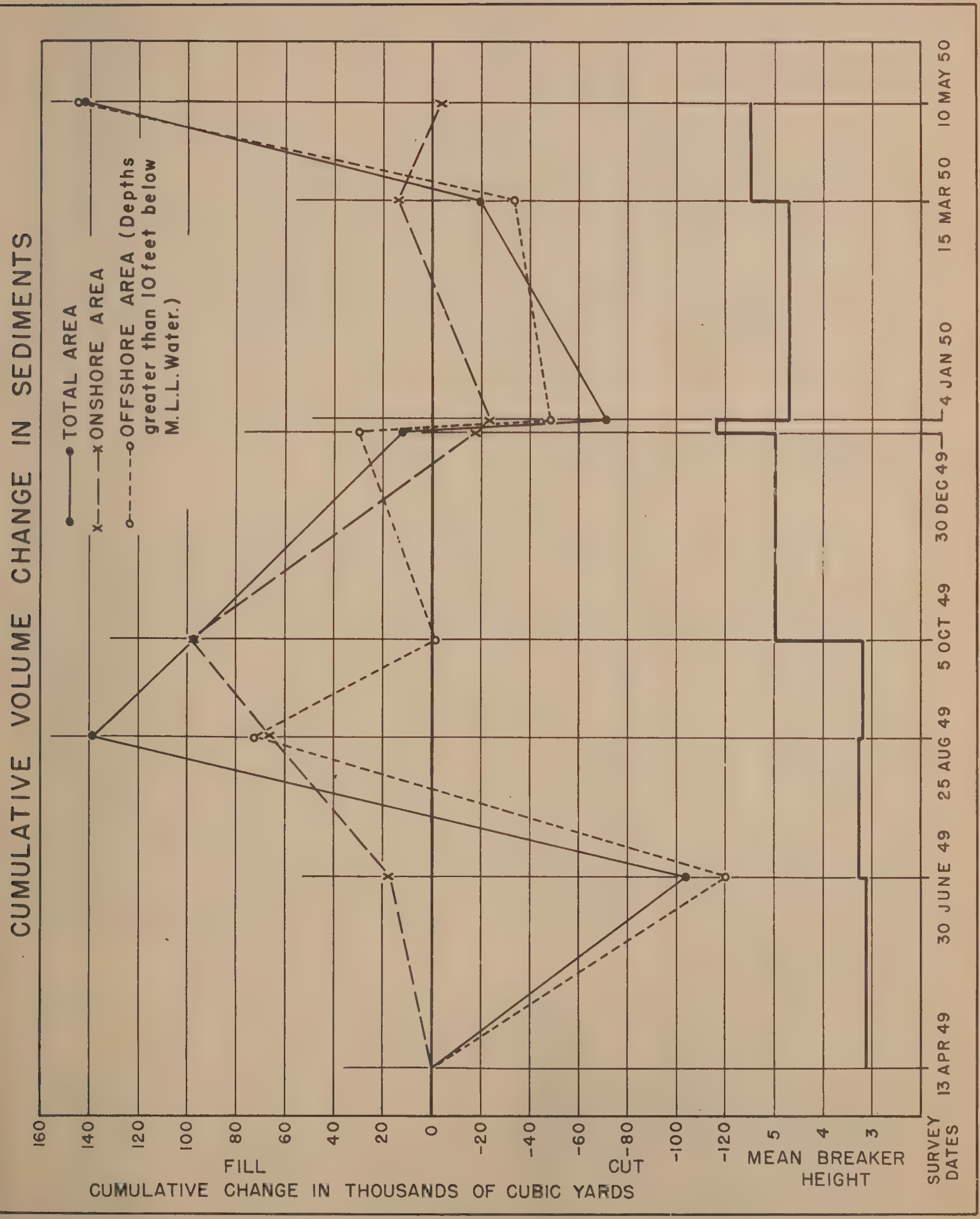


SAND LEVEL CHANGES BETWEEN
15 MAR — 9,10 MAY 1950

CONTOURS IN FEET

0
1000
2000
SCALE IN FEET
CUT >3 FEET
CUT 2-3 FEET
CUT 1-2 FEET
CUT 0-1 FEET
FILL 1-0 FEET
FILL 2-1 FEET
FILL 3-2 FEET
FILL >3 FEET
50
100
200
25
10
RANGE "A"
"A-1"
SCRIPPS PIER
"B"
"C"
"D"
"E"
"F"
"G"
RANGE "H"
M.L.L.W.
0
POINT LA JOLLA
N

FIGURE 15


CUMULATIVE VOLUME CHANGE IN SEDIMENTS

probably more accurate than the offshore because a larger portion of the inshore surveys was made with transit and range pole, which eliminates the error due to small fluctuations of sea level which are not shown on the Coast and Geodetic Survey tide gauge located at Scripps Pier.

In considering the maps it should be noted that the eastern margin represents the sea wall except in a small area where there are alluvial cliffs forming the coast. The average height of sand along this coastline is 9 feet (above mean lower low water) although this varies seasonally. The changes in sand level shown on the isopleth maps (figures 8-14) represent the net changes that occurred during each survey period (periods averaged approximately 45 days). It should be emphasized, however, that any large waves which occurred directly before the survey may have had much more influence on the depths than all preceding wave conditions. Conversely a long interval of small waves before a survey may have eliminated the effect of large waves in the earlier part of the period.

Table I gives in summary form, the net changes estimated between each survey. The significance of the changes can be considered to best advantage by a separate discussion of each period.

13, 14 April to 30 June, 1949 (Figure 8) - During this period the least satisfactory correlation with wave type can be made because relatively few wave periods were obtained before May 9th and no data is available on the direction of wave approach. Despite relatively small breakers the net change is estimated as a cut of 103,800 cubic yards, but the zone inside the 10 foot isobath shows a net fill of 17,080 cubic yards and the beach above mean lower low has undergone a fill along the entire length of the beach. Judging from the cut which borders the seaward side of this filled zone there has been a transfer of material landward from the shallow water area near shore. This is apparently related to the relatively small waves which existed during this period (Figures 2 and 5). It will be noted that the dividing line between cut and fill occurs nearer the shore and in shoaler water along the southern lines than in the northern lines. This may be attributed to the canyon effect on the wave orthogonals which produces smaller breakers inside the canyon head (Munk and Traylor, 1947). As a result of these smaller waves the transfer of sediment shoreward took place at shoaler depths, the fulcrum presumably coming at a depth close to the breaker line during the times of major waves.

The net cut of 120,880 cubic yards in the zone outside the 10-foot isobath is not as easy to understand, particularly during a period of relatively small waves. However, the changes in the outer zone, as will be seen, have in other cases a more apparent relationship to waves. During this interval as in most of the others the sand outside appears to have shifted more in a direction parallel to the shore than normal to it. It may well be that there were periods of large waves in some of the short gaps in wave data in April and that these waves accounted for the net deepening and for the shift to the south which is indicated.

TABLE I. Net Changes in Volume Between Each Survey.

Survey Period*		Inshore Area in cu. yds.		Offshore Area (Depths greater than 10 ft. below MLLW) in cubic yards.		Total Area in cu. yds.	
13-14 Apr	to 30 June-1 July 49	Fill	17,080	Cut	120,880	Cut	103,800
30 June-1 July	to 25-26 Aug 49	Fill	49,000	Fill	193,680	Fill	242,680
25-26 Aug	to 5-6 Oct 1949	Fill	32,820	Cut	73,800	Cut	40,980
5-6 Oct	to 30 Dec 49	Cut	116,260	Fill	31,120	Cut	85,140
30 Dec 49	to 3-6 Jan. 1950	Cut	6,050	Cut	78,230	Cut	84,280
3-6 Jan	to 15 Mar 1950	Fill	37,760	Fill	14,640	Fill	52,400
15 Mar	to 9-10 May 1950	Cut	17,370	Fill	179,350	Fill	161,980

*Multiplicity of dates indicates that the survey was not completed in one day.

30 June -1 July to 25 August 1949, (Figure 9) - During this second period the breakers averaged about the same as in the first one so far as one can tell from available information. The wave periods differ somewhat in that there are more long period waves represented, probably the southerly swell which becomes dominant in this area in summer.

During this summer period a net fill of 242,680 cubic yards was computed. The net fill inside the 10 foot isobath amounted to 49,000 cubic yards, being especially pronounced along "D" Range which frequently represents the zone of maximum wave convergence over the ridge between the two submarine canyon heads. The pronounced summer fill of the beach along this range has been noted for many years. The zone of cue outside the fill is still evident except along "D" Range where fill is virtually continuous. It is notable that the pivotal line has moved shoreward along ranges "A-1" and "B" and also that there has been a small cut at the top of the beach along ranges "A-1" and "C". The changes in deeper water are quite different from the earlier period since they involve a net gain of 193,680 cubic yards, much more than in the nearshore area. Deposition apparently occurred over most of the area although small losses are indicated on the outer portions of lines "B", "D" and "E".

25, 26 August to 5, 6 October 1949 (Figure 10) - In the third period the trend changed to a net loss of 40,980 cubic yards although the fill continued inside. The breakers were small, never exceeding 5 feet. The abundance of long period waves increased, and the direction of wave approach was distinctly more from the south than in the earlier periods.

Inside the 10 foot isobath there was a net fill of 32,820 cubic yards. In this area there are alternating bands of cut and fill which extend roughly parallel to the breaker line so that they bend shoreward at the canyon head.

Outside of the 10-foot isobath there was a cut of 73,800 cubic yards. Although there was fill at some points along each of the lines in deeper water, except line "A-1", the change is largely in the nature of a lateral shift. The small waves of the period could not be expected to have any appreciable effect on the deeper area although their longer period would tend to give them greater effect at depth. It seems likely that currents not directly related to surface waves shift materials at these greater depths during periods of small surface waves.

5, 6 October to 30 December 1949 (Figure 11) - In the fourth period the wave conditions had changed to a marked degree. Six days have recorded breakers of 10 feet or more in height whereas no 10-foot breakers were observed in any of the preceding periods. Four of these days of high waves had higher-high tides slightly above the average for the locality. The direction of the waves had changed so that a northwest and west-northwest approach had become important in contrast to the southerly approach of the preceding periods. The wave periods were somewhat shorter than in the preceding months particularly during the times of largest waves.

The depth changes in the shoal area show a marked effect of these large waves. A net cut of 116,260 cubic yards is estimated for the zone inside the 10-foot isobath. This cut was particularly pronounced at the convergence (Range "D") and extended seaward farther in the zone north of the canyon. This effect may represent a combination of the larger waves in this convergence area and a southerly transport of sand due to the northwesterly wave approaches. However, it will be observed that the cut along the shore was general. One net effect of this cut was the development of bars and troughs in the northern zone, the troughs representing zones of greater cut and the bars less cut. Outside the excavated zone there is a corresponding fill which occupies about the same width, measured normal to the shore, as does that zone of excavation, but does not balance the cutting since it is of much smaller degree.

The net change in the zone outside the 10-foot isobath is a fill of only 31,120 cubic yards, which leaves a net cut for the total area of 85,140 cubic yards. It is notable that the fill in this outer zone is largely found directly outside the inner cut and thus suggests a displacement outward of the inner sediment. The indications are that the outer area as a whole was undergoing cut since 60% of the area has deepened although the volume of the removed material is smaller than for the fill elsewhere.

30 December 1949 to 3-6 January 1950 (Figure 12) - The fifth period, far shorter than the others, was given this short interval in order to test the effect of the large waves of January 3rd. These waves accompanied a northwest blow which was one of the most violent of the entire period of this study. On this day the higher-high tide was 6.5 feet which is well above the average. The breaker heights are not listed as being as high as on several other occasions although these heights are most difficult to estimate during blows with short period waves. The waves were closely related to a severe wind storm which is rather unusual in the southern California area. The waves subsided so quickly that it was possible to repeat the survey two days after the maximum waves and the beach was surveyed during the end of the storm. Since the preceding surveys had taken place four days before the large waves, the changes may be presumed to have resulted largely from this particular storm.

Along the shore where the profiles were started on the day of the storm two striking results are indicated. In the first place the sand was cut from the north portion of the beach and was built up over a wide zone shoreward of the submarine canyon head. This shift was certainly the effect of the northwest approach of the short period waves, a condition which sets up strong longshore currents to the south (Shepard and Inman, 1950). A southerly longshore current with a velocity of 0.7 knots was measured from Scripps Pier during this storm. In the second place the bars and troughs of the northern shore zone had disappeared and an even slope was developed. The contrast in profiles is shown in the inset to Figure 12. This straightening of slope has been observed in many other storms on both the east and west coasts of the United States.

During this storm the net effect inside the 10-foot isobath was a cut, but only to the extent of 6,050 cubic yards. The small amount of this cut is perhaps understandable in view of the series of periods of large waves which had preceded this particular storm. These large waves had presumably brought the beach somewhat into equilibrium with large wave conditions.

The most surprising feature about the short period change is that it was clearly indicated out in deep water with a cut of 78,230 cubic yards. The nature of these deep changes extending to at least 100 feet, is similar to that near shore in that the northern part of the shelf was cut about one foot on the average and the southern portion was filled to about the same height but over a considerably smaller area than was involved in the cut. Therefore, one can conclude that in a storm of this type the waves, or the currents set up by the waves, are effective in producing large shifts of sediment out to at least 100 feet below sea level. A considerable portion of the sediments were presumably washed into the canyon and therefore lost to the area.

3-6 January to 15 March 1950 (Figure 13) - During the mid-winter period the waves were somewhat smaller than during the preceding three months. On two days breakers reached 10-foot heights, but on both occasions there were neap tides so that the effect on the upper beach would tend to be depositional (Shepard and LaFond, 1940). The largest waves came from west and northwest as in the period from 5 October-30 December, however both of these surveys were preceded by more than a week of small waves.

The area shows a net fill during this period amounting to a total of 52,400 cubic yards. Inside the 10 foot isobath 37,760 cubic yards of fill was estimated with the largest fill in the surf zone on "A-1" and "D" Ranges. The area inside the canyon which had undergone fill during the early January storm shows a fairly consistent deepening, presumably the result of the removal of the excess sand brought in by the northwesterly approaching waves of the preceding period.

15 March to 9-10 May 1950 (Figure 14) - During the last period of the surveys the waves continued to be large. On three occasions they exceeded 10 feet. The wave periods were short for the most part. The large waves had varying directions of approach.

Inside the 10 foot isobath the net change was a cut, but only to a small extent, 17,370 cubic yards. The cut is pronounced at the north end of the zone reflecting the northwesterly approach of a recent storm. This cut is nearly balanced at the south end of the nearshore area.

The net change outside the 10-foot isobath involves a large fill, 179,350 cubic yards. Here also the sediment has shifted to the south although this is not as evident as in the case of the 3 January storm. The fill appears to be quite well substantiated. The net fill for the entire area suggests an outside source of sand during this period. It will be noted that a similar and larger fill for the entire area occurred at a later period in 1949 but in that case the waves had been small.

Summary and Conclusions

The preceding description of observed changes of sand level at La Jolla demonstrates, despite limitations, that changes in level take place at all seasons across the entire area from the beaches down to depths of at least 100 feet below mean lower low water. The beach and shallow water changes appear to show a general relationship to the character of the waves during each period. The onset of the first large waves in the fall produces a general cut amounting to several feet and most of the sand which has been removed is redeposited directly outside the cut portion. As soon as the shallow area and the beach have become adjusted to large wave conditions, additional cut becomes negligible, although there are signs of shifting laterally along the shore in response to direction of wave approach. In the spring and summer small waves result in a return of the sand to the beach and shallow water area, thus completing the cycle.

In deep water the sand shifts are more complex and less clearly related to the observed waves of the period. There is considerable evidence that the chief movements of sand are roughly parallel to the coast rather than normal to it. It is notable that the first period of large waves was accompanied by a small increase in the total sand outside, but a very large decrease followed during the severe 3 January storm. It is also somewhat surprising that the sand on the outside was built up during the second spring period when the waves were large, whereas the building in the previous year occurred during a summer period of small waves. Presumably some type of current not directly related to waves produced some of the sand movement.

It is understandable that the offshore area should lose sand during periods of large waves. The shifting of the sand laterally in either direction in this particular area should result in a considerable amount of sediment being carried into the submarine canyons. Thus the waves of 3 January 1950 appear to have shifted considerable quantities of sand to the south and presumably much of this was carried into La Jolla Canyon. It is difficult to understand how sand could be returned subsequently to the shelf out of the canyon because of the steepness of the slopes. Therefore, the rebuilding of the shelf apparently indicates a source of sand either from inshore or from one of the other shelves around the heads of the canyons. There was no indication of significant depletion of the beach or shallow area during either period of large offshore fill. On one occasion there could have been no supply from the erosion of the alluvial cliffs or from running water coming down the only shallow valley which cuts the alluvium. On the other occasions both of these sources might have provided a small amount of material, but a calculation of the rate of retreat of the alluvial cliffs during the entire year would only provide approximately 200 cubic yards of sand and it is doubtful if the small rains carried in an equal amount. No appreciable source of sand from the south of La Jolla Canyon seems possible because the shelf in that area has very little sand and almost all of it is much coarser than that in the area under discussion.

By elimination, the shelf north of Scripps Canyon appears to be the only good source of sand. This shelf has a much larger supply of sand provided from erosion of the high cliffs and from the streams which flow down the numerous gullies and canyons during the occasional rains. It seems perfectly possible that sand from these sources is shifted along the coast past the canyon head. The faster rate of fill which has been observed in the branches of Scripps Canyon as compared to the branches of La Jolla Canyon (Sheperd, 1951) is further indication of the large supply of sediment coming from the north of Scripps Canyon. Whenever the introduced sand exceeds the sand lost from the shelf between the canyons, the depths in the outer area should decrease. Possibly the shifting past the canyon head is started in the fall by the first northwesterly approaching waves but does not affect the surveyed portion of the intercanyon area until considerably later. The mechanics of this shift are certainly not very clear and it seem advisable to make a further study of this process.

Acknowledgments

Most of the work was supported by appropriations from the Beach Erosion Board. The writers desire to express appreciation also for the valuable assistance in field and laboratory of Miss Ruth Yound and Mr. Donald B. Sayner.

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Scripps Institution of Oceanography, Bull., Tec. ser., v. 6:3.

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REPRINT FROM
CALIFORNIA FISH and GAME
"CONSERVATION OF WILDLIFE THROUGH EDUCATION"
VOLUME 37 OCTOBER, 1951 No. 4

AN ABNORMAL CARP, *CYPRINUS CARPIO*, FROM CALIFORNIA WATERS[1]

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In early October, 1949, a peculiar fish was caught on hook and line in an irrigation canal east of El Centro, Imperial County, by Mr. Williams of Brawley, California. Captain Willard Greenwald, of the Bureau of Patrol and Law Enforcement, California Division of Fish and Game, who tentatively identified the specimen as a carp, brought it to the Scripps Institution of Oceanography for confirmation. In spite of its obvious deformity, the fish was found to agree in all essential respects with *Cyprinus carpio* Linnaeus.

The carp and some of its close relatives are notably variable in body form and structure. From a single species of this group (*Carassius auratus*) have been produced, by careful breeding, the widely divergent varieties of the common goldfish. Many of the peculiar domestic forms of the goldfish are paralleled by similar types of carp. The body form and rate of growth of the carp are known to be extremely sensitive to the effects of environment (Kirpichnikov, 1945) and the specimen here

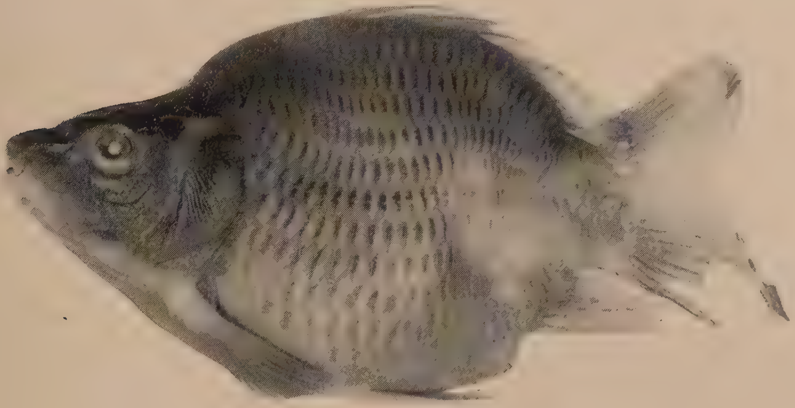

FIGURE 167

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[1] Submitted for publication January, 1950.

[2] Contributions from the Scripps Institution of Oceanography, New Series, No. 535. The senior author is now Director, Virginia Fisheries Laboratory, Gloucester Point, Virginia. The junior author has returned to the Pacific Biological Station, Nanaimo, B. C., from which laboratory he was on educational leave.

described (Figure 167) is similar in outward appearance to the "mast-form" described by Wunder (1939).

An X-ray photograph showed that the deformity is not confined to external features. The vertebral column is reduced in length by the fusion of adjacent centra in several regions, and at about its midlength at least 10 centra are fused in a solid segment. Malformations occur in at least nine regions of the backbone. Two striking features are apparent: (1) the identity of the individual centra is preserved in the neural and haemal processes, which are present in numbers normal for the species, and (2) the fused groups of vertebrae, separated by distinct articular spaces, are, with the exception of the major segment of 10 centra mentioned above, each approximately as long as a single vertebra.

Fusions and deformities involving a limited number of vertebrae are not uncommon in natural populations of fishes. In Atlantic (*Clupea harengus*) and Pacific herring (*Clupea pallasi*) such anomalies are found in as many as 14 percent of the individuals in a sample (Ford and Bull, 1926; McHugh, 1942). These occur most commonly at the posterior end of the vertebral column, and are characterized by a duplication of the neural or haemal spines or both, in association with a centrum that is typically single. Schmidt (1921) found that double vertebrae of this type were more common in trout (*Salmo trutta*) with low numbers of centra, and assigned the numerical value 1.5 to such vertebrae. As pointed out by McHugh (1942), fusions in other parts of the vertebral column differ in structure and probably in origin from those at the posterior end. It is obvious that in the carp described here the true number of vertebrae is indicated by the vertebral processes, and that a numerical adjustment such as proposed by Schmidt would result in a vertebral count that would be ridiculously low for the species.

The external meristic features also correspond with those of the normal carp, as indicated by the following fin-ray and scale counts: dorsal III, 20; anal III, 5; pectoral 16; pelvic 9; scales 6-37-6. The foreshortening of the body has its most marked effect externally in the region overlying the section of maximum coalescence of vertebral centra, at a point about midway between the insertions of the pelvic and anal fins In the region of the lateral line, from this point backward, the scales are crowded together so that less of their area is exposed. Under the microscope these have the appearance of regenerated scales, their centers being granular in texture with no regular pattern of circuli. The scales in the anterior portion of the body appear normal, and an attempt was made to determine the age of the fish. Although the annuli are not clearly marked, the fish was approximately in its sixth year of life. In length (159 mm.) it was therefore much smaller than a normal carp of this age. Because the caudal peduncle is extremely short, the median fins, when depressed, overlap the caudal fin (Figure 167).

Malformations of this type are occasionally seen in many species of teleost fish. A somewhat similar abnormality in a carp from the upper Illinois River has been described by O'Donnell (1945). In his specimen the last eight precaudal and the 17 caudal centra were completely fused. He concludes that the condition resembles arthritis deformans as found in man and other mammals.

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51050-1 10-51 475

REPRINT FROM

CALIFORNIA FISH and GAME

"CONSERVATION OF WILDLIFE THROUGH EDUCATION"

VOLUME 37 OCTOBER, 1951 No. 4

AN ANNOTATED LIST OF THE CLUPEOID FISHES OF THE PACIFIC COAST, FROM ALASKA TO CAPE SAN LUCAS, BAJA CALIFORNIA[1]

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California Division of Fish and Game

The Cooperative Sardine Research Program, in which vessels and personnel of the California Division of Fish and Game, the U. S. Fish and Wildlife Service and the Scripps Institution of Oceanography are participating, is conducting surveys of spawning of sardines and studies of the distribution of larval, young and adult sardines along the Pacific coast from Oregon south to the tip of Baja California. Within this range a number of more or less closely related clupeoids are found, some in considerable abundance. The larvae of these species are so extremely similar in general appearance that their identification is not always easy. The characters by which these early stages may be recognized are now under investigation.

During the past few years many samples of clupeoids have been taken on a number of cruises, particularly along the Pacific coast of Baja California. Insofar as we can determine, the ranges of six species have been extended northward. In view of the rapidly increasing interest in the fishes of this section of the coast, and of the inadequate ichthyological knowledge of the southern waters, it seems appropriate that the available records be reviewed.

Only those families commonly encountered in bays or within a few miles of shore are treated here. For this reason the Alepocephalidae are not included.

For distributional records, reference has been made to several publications of a general nature, namely, Barnhart (1936), Clemens and Wilby (1946), Fowler (1944), Hildebrand (1943), Jordan and Evermann (1896), Meek and Hildebrand (1923) and Walford (1937). Where the range quoted in the present paper does not agree with that of the authors mentioned above, the appropriate literature reference or data bearing on recent collections are given. Unless otherwise indicated, the collections listed have been made on cruises of vessels of the Scripps Institution of Oceanography or of the California Division of Fish and Game.

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[1] Submitted for publication February, 1951.

[2] Contributions from the Scripps Institution of Oceanography, New Series, No. 536. Dr. McHugh is now Director, Virginia Fisheries Laboratory, Gloucester Point, Virginia.

FAMILY ALBULIDAE—THE BONEFISHES

Albula vulpes (Linnaeus)—bonefish

Range. San Francisco Bay, California (Myers, 1936), to Panama.

Recent Collections. California: Oceanside, May 5, 1948; Newport Bay, October 9, 1949. Baja California: Turtle Bay, February 9, 1948; Santa Maria Bay and Magdalena Bay, April 15 and 16, 1950, respectively.

FAMILY CHANIDAE—THE MILKFISHES

Chanos chanos (Forskal)—milkfish

Range. Baja California to Panama. Although there have been no definite California records since a small planting of fish from Hawaii was made in the San Francisco region in 1877, the species has been taken off the west coast of Baja California (Clark, 1929) and is abundant in the Gulf of California.

FAMILY DUSSUMIERIIDAE—THE ROUND HERRINGS

Etrumeus othonops (Eigenmann)—California round herring

Range. Central California (Phillips, 1951) to the Gulf of California.

Recent Collections. California: off San Diego, June, 1947; Santa Cruz Island, November, 1949; Los Angeles Harbor and Santa Monica Bay, March, 1950. Baja California: San Roque Bay, February 8, 1948; Magdalena Bay, February 15 and August 15, 1949; Sebastian Viscaino Bay, September 29, 1949; Ballenas Bay, April 11, 1950.

FAMILY CLUPEIDAE—THE HERRINGS

Clupea pallasi Cuvier and Valenciennes—Pacific herring

Range. North coast of Eurasia, and from Bering Sea to northern Japan and to San Diego, California. This species is of great commercial importance in the waters of Alaska and British Columbia, where it reaches its greatest abundance. A number of local populations appear to represent distinct races. A single record from Tenacatita, Mexico (Seale, 1940), was almost certainly based on a mistaken identification.

Recent Collections. California: many taken in bait hauls, Los Angeles Harbor, winter of 1949-50; other schools hit during seismic operations, Santa Barbara region, 1948 and 1949; San Diego Bay and off Point Loma, 1946 to 1950.

Sardinops caerulea (Girard)—Pacific sardine

Range. Southeastern Alaska to the Gulf of California. Probably the most abundant clupeoid on the Pacific coast, its distribution centers off Southern California and northern Baja California. At least two distinct populations exist.

Recent Collections. Many recent collections have been made within this range.

Alosa sapidissima (Wilson)—shad

Range. Introduced in California waters in 1871, the species now ranges from Kodiak Island, Alaska, to San Diego, California (Welander, 1940).

Recent Collections. California: Santa Barbara region, 1948 and 1949; Huntington Beach, October 28, 1949.

Harengula thrissina (Jordan and Gilbert)

Range. San Juanico Bay, Baja California, and the Gulf of California, to Panama. This semitropical species probably does not range much farther up the outer coast of the peninsula. The known range is extended northward more than 200 miles.

Recent Collections. Baja California: San Lucas Bay, October 7, 1949; Santa Maria Bay, April 14, 1950; San Juanico Bay, April 12, 1950.

Lile stolifera (Jordan and Gilbert)

Range. Ballenas Bay, Baja California, to Peru. The known range is extended northward some 300 miles.

Recent Collections. Baja California: San Juanico Bay, September 26, 1948, and April 12, 1950; Coyote Lagoon, Ballenas Bay, September 25, 1948.

Opisthonema libertate (Gunther)—thread herring

Range. San Pedro, California, to Peru.

Recent Collections. California: San Pedro, April, 1950. Baja California: Ballenas Bay, April 11, 1950; San Juanico Bay, September 30, 1948, April 12 and 13, 1950; Santa Maria Bay, April 15, 1950; Magdalena Bay, September 28, 1948, and February and April, 1950.

FAMILY ENGRAULIDAE—THE ANCHOVIES

Engraulis mordax Girard—northern anchovy

Range. The ocean subspecies, *Engraulis mordax mordax*, ranges from northern British Columbia to Cape San Lucas, Baja California. The bay form, *Engraulis mordax nanus*, has been recorded only from the San Francisco Bay region, California (Hubbs, 1925).

Recent Collections. Numerous samples from southern British Columbia to southern Baja California examined in a study of local populations (McHugh, in press).

Anchovia magdalenae Hildebrand

Range. Known only from Magdalena Bay, Baja California. Described from two specimens and not since recorded.

Anchoa compressa (Girard)—deep-bodied anchovy

Range. Morro Bay, California, to Todos Santos Bay, Baja California. The known range is extended northward from Point Conception.

Recent Collections. California: Morro Bay, July 19, 1950 (collected by Boyd W. Walker); many samples from Mission Bay and San Diego Bay. Baja California: Todos Santos Bay, December 20, 1945, Estero de Punta Banda, July 12, 1946.

Anchoa mundeoloides (Breder)

Range. Almejas Bay, Baja California, and Gulf of California to Panama. A single specimen was collected in Almejas Bay from the Division of Fish and Game research vessel "N. B. Scofield" March 3, 1939, and deposited in the Stanford Natural History Museum collection. Not taken on the outer coast since that date.

Anchoa helleri (Hubbs)

Range. Gulf of California. A single specimen recorded by Hildebrand (1943) from Cape San Lucas, Baja California, is the only record from the southwestern limit of the Gulf. Hildebrand suggested that the collection may have been incorrectly labelled.

Anchoa ischana (Jordan and Gilbert)

Range. Gulf of California (Boyd W. Walker, ms.) to Acapulco, and to Magdalena Bay, Baja California. We have not taken this species from the outer coast of the peninsula.

Anchoa cultrata (Gilbert)

Range. Santa Margarita Island, off Magdalena Bay, Baja California. According to Hildebrand (1943) this species is known only from the original description, based on a single specimen which cannot be found. It resembles both *Anchoa ischana* and *Anchoa naso.*

Anchoa exigua (Jordan and Gilbert)

Range. San Juanico Bay, Baja California, to Panama. The known range is extended northward and westward from Mazatlan, Mexico.

Recent Collections. Baja California: San Juanico Bay, September 30, 1948; Magdalena Bay, February 15, 1949, and April 15, 1950.

Anchoa curta (Jordan and Gilbert)

Range. San Juanico Bay, Baja California, to Ecuador. The known range is extended westward from the mouth of Rio Yaqui, on the east side of the Gulf of California.

Recent Collections. Baja California: a small sample from San Juanico Bay, April 12, 1950, the first record from the Pacific coast of the peninsula.

Anchoa delicatissima (Girard)—slough anchovy

Range. Los Angeles Harbor, California, to Todos Santos Bay, Baja California.

Recent Collections. California: Brighton Beach, Terminal Island (Clothier, 1950); Santa Catalina Island, August 20, 1948. Baja California: Estero de Punta Banda, September 1, 1949.

Anchoa naso (Gilbert and Pierson)

Range. San Juanico Bay, Baja California, and Gulf of California (Walker, ms.) to Peru. The known range is extended northward 18 degrees of latitude from the Pacific coast of Panama, a distance of almost 2,000 miles in a northwesterly direction.

Recent Collections. Baja California: San Juanico Bay, September 30, 1948; Santa Maria Bay and Magdalena Bay, April 14 and 15, 1950.

Anchoviella scitula (Fowler)

This nominal species was described from a single specimen taken in San Diego Bay, California. According to Hildebrand (1943) who examined the type, it differs very slightly from *Anchoa exigua*, a species which might migrate northward during warm periods. The possibility also exists that the original description may have been based on an aberrant specimen of *Engraulis mordax*, for anal fin-ray counts as low as 12 (normally 20 to 25) have been encountered in this anchovy. Gill-raker counts in *Engraulis* also vary considerably, and the number increases throughout life (McHugh, in press). In spite of the numerous collections that have been made in the San Diego area in recent years not a single specimen referable to *Anchoviella scitula* has been taken. It seems highly unlikely that the species is valid.

***Cetengraulis mysticetus* (Gunther)—anchoveta**

Range. San Pedro, California, to Peru.

Recent Collections. California: San Diego Bay, December, 1947, to January, 1948. Baja California: Magdalena Bay, February, 1949.

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51050-2 10-51 475

Reprinted from The Condor, Volume 53, September-October, 1951, Number 2, pp. 221-227

PERSISTENCE OF A RARE COLOR ABERRATION IN THE HEERMANN GULL

By CARL L. HUBBS and GEORGE A. BARTHOLOMEW, JR.

On February 8, 1948, while aboard the Schooner "E. W. Scripps," stormbound in Bahía Tortugas, Baja California, we observed in a flock of Heermann Gulls (*Larus heermanni*) two immature individuals with a patch of white on each wing. The wing pattern of white on dark gray gave these birds in flight a flashing appearance suggestive of Willets. In one bird the white patch extended entirely across each wing and therefore covered several quills, probably secondaries. In the other bird some primary coverts and only two or three quills, on each wing, were white.

A similar individual was twice observed on September 24, 1950, on the beach just north of Punta Cabras, northwestern Baja California. It had an oblong patch of clear white near the bend of each wing, parallel to and well within the front margin. The only other similarly marked Heermann Gull that either of us has seen recently in the field was watched on November 9, 1950, at Playa del Rey, California. Its completely symmetrical white wing patches resembled that shown in figure 1.

These isolated observations assume significance when it is recalled that essentially similar color variants have been observed in this species throughout a wide geographic range sporadically for nearly a century (Swarth, 1924). Most published reports date from 1918 to 1924 and none seems to have appeared during the past quarter century. The persistence of the rare aberration, however, is proved by unpublished observations included in the list on pages 222-224.

The sporadic repetition of this striking variation (Taverner, 1918) suggests that its cause lies in some such genetic mechanism as (1) recurrent mutation; (2) the occasional chance mating of the rare individuals that carry the recessive gene or genes which in homozygous combination produce the anomaly; (3) the infrequent phenotypic expression of a gene or of genes having low penetrance or low expressivity; or, possibly, (4) the rare atavistic retention of an ancestral trait.

Whatever its genetic mechanism may be, the aberrant pattern has remained very rare throughout the century of observation. The two patterned individuals seen on February 8, 1948, were the only abnormal ones among hundreds. The one observed on September 24, 1950, was unique among 194 counted on the same beach. The one watched on November 9, 1950, was the only variant in a flock of about 400. The proportion must be lower than one in several hundred, however, for only these four abnormal individuals have been seen by us among the many thousands checked in 1948, 1949 and 1950 at various localities in California, along the outer coast of Baja California, and at several points in the Gulf of California. Lewis Wayne Walker tells us that he does not recall having seen any such variants among the myriads of Heermann Gulls that he has observed and photographed during several visits, some as long as three weeks, to the breeding colonies on Isla Raza in the Gulf (Walker, 1951). On the same island van Rossem (personal communication) saw about 20 of the variants among the many thousands observed in 1925. On the label of a white-blotched wing that he collected at Isla Raza in 1930 (fig. 1), van Rossem wrote: "this type of wing present in proportion of about 1 to 1000." On the 1925 trip he saw only one such bird in the breeding colony on Isla San Jorge and none in the colony on Isla Ildefonso, both also in the Gulf of California. In 1949 and in other years Ed N. Harrison and others have studied and photographed the breeding Heermann Gulls on Isla San Jorge without noting a single

Contribution No. 537 of the Scripps Institution of Oceanography.

bird with white wing patches. Bancroft's (1932:341) estimate of one such aberration per thousand birds for the Raza colony in 1925, though agreeing with van Rossem's estimate, was probably excessive. A frequency of only one in ten thousand seems more reasonable.

We have, it is true, located 20 variants of this type among the 616 specimens of the species, downy young excluded, in the nine collections examined (see p. 226 for explanation of abbreviations): LACM, 8 among 108; MVZ, 5 among 98; SDSNH, 3 among 29; DC, UCLA, 2 among 16; MCZ, 1 among 75; CAS, 1 among 168; USNM, 0 among 25; UMMZ, 0 among 29; AMNH, 0 among 68. It is obvious, however, that the striking variants have been collected and preserved in numbers disproportionate to their actual frequency in nature. The clustering of records around 1910 and 1918, respectively, probably reflects the especially active collecting then of R. H. Beck and of George Willett.

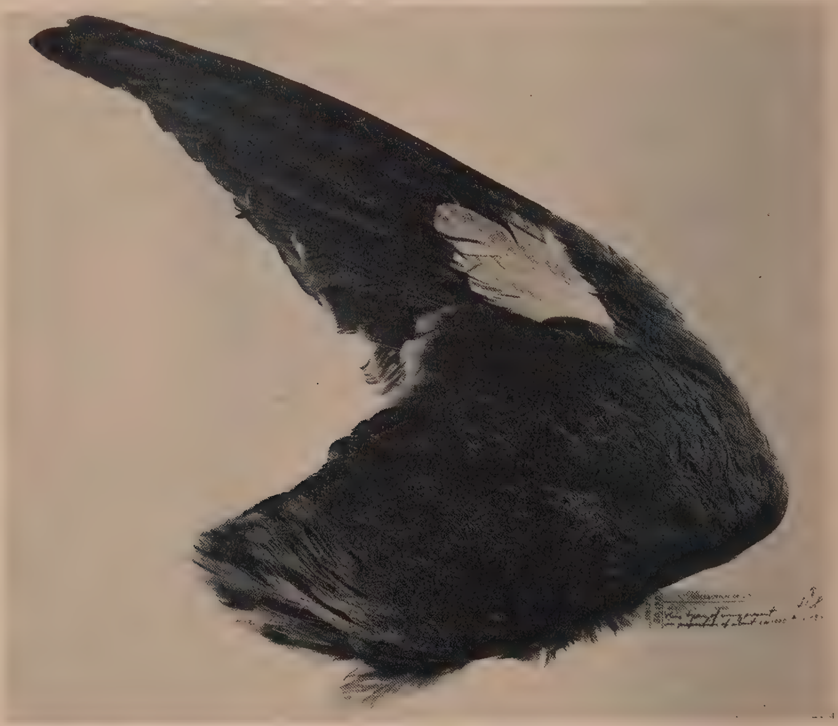

Fig. 1. Wing of Heermann Gull from Isla Raza, Gulf of California (specimen no. 23), showing white blotch on primary coverts.

Known records of white wing patches.—The abbreviations for the collections examined are explained in the acknowledgments, page 226. Specimens are listed in order of date of collection or of observation. Because of the complicated seasonal as well as age changes in plumage, the age estimates are subject to error.

1. February 4, 1862: immature female, perhaps in second year; San Diego, California; J. G. Cooper; MVZ 4418, prepared with wings extended. This is almost certainly the bird independently reported, on the basis of information found in the correspondence of the collector, but without adequate data, by Deane (1879) and by Swarth (1924); both authors quoted Cooper as saying that

the large white patch on each wing extended across the "secondary quills," whereas the white is actually on the greater primary coverts (see table 1).

2. January 4, 1897: adult male in winter plumage; Monterey, California; Alvin Seale; MCZ 246919 (not previously recorded). James L. Peters describes the white markings on this bird as follows: On the left wing, "the outer six greater primary coverts are white, although the third one has only a little white freckling on the outer web. The median primary coverts are white—some of them with a small amount of dusky freckling. Almost all the secondaries are white—the inner ones with a small amount of dusky freckling and the outer ones with a good deal of dusky on the outer webs. There doesn't seem to be much sense to the arrangement of the dark areas." On the right wing, "the outer secondaries contain the most white, while the innermost ones are normally colored and the median primary coverts also contain a great deal more of the dark feathers."

3. October 18, 1909: immature female; Monterey Bay, California; R. H. Beck; CAS 15886 (not previously reported. (See table 1.)

4. August 10, 1910: immature female, perhaps in second year; vicinity of Point Pinos, Monterey County, California; Beck; MVZ 18241 (not previously reported). Large white area on left wing, smaller on right (table 1).

5. November 28, 1910: immature male, perhaps in second year; Monterey Bay, California; Beck; MVZ 18265 (not previously reported). (See table 1.)

6. 1911: several observed at Redondo, California (Hubbs, 1919). "Each of these had a large squarish white blotch symmetrically located near the angle of each wing, in some cases more definitely and more extensively developed on the one side than on the other."

7. January 30, 1912: adult female; Hyperion, Los Angeles County, California; George Willett; LACM 1105 (Willett, 1918). Specimen re-examined.

8. March 16, 1912: immature female, perhaps in second year; La Paz, Baja California; W. W. Brown; MVZ 106897 (not reported previously). Two primary coverts partly white on right wing, none on left (table 1).

9. January 26, 1916: adult female; Hyperion Beach, California; L. E. Wyman; LACM 14027 (reported by Willett, 1918, as having "two white feathers in primary covert of one wing, but none in other"). Specimen re-examined (table 1).

10. February 25, 1916: subadult or winter male; Pacific Beach, California; Frank Stephens; SDSNH 6770 (not previously reported). Extremely large white areas in primaries as well as on greater primary coverts (table 1).

11. August 14, 1917: subadult female; Alert Bay, Vancouver Island, British Columbia; Museum of the Geological Survey of Canada (reported by Taverner, 1918, as having four outer primary coverts of one wing and two of the other pure white).

12. January 18 to February 5, 1918: three adult females and one adult male; Hyperion, California; George Willett; LACM 2127, 2128, 2199, 2210 (reported with no. 7 by Willett, 1918, as having a white patch on each wing). Specimens re-examined; no. 2128 has a scattering of white feathers on the abdomen.

13. June 21, 1918: one observed at Pacific Grove, California (Hubbs, 1919; reported with no. 6).

14. October 21, 1918: adult female; Hyperion; L. E. Wyman; LACM 2723 (not previously reported). Wyman noted: "primary coverts white; faint touch of white across abdomen."

15. November 22, 1918: adult female; Hyperion; Willett; LACM 2604 (not previously reported). Five primary coverts largely white, two on the left wing and three on the right.

16. January 30, 1920: adult female; Camp Banning, Santa Catalina Island, California; A. J. van Rossem; DC, UCLA H269 (reported by Dickey and van Rossem, 1923, as having "the aberrant white primary coverts"). Specimen re-examined (table 1).

17. February 17, 1921: one seen at Santa Catalina Island "displayed this same covert-pattern" (Dickey and van Rossem, 1923).

18. Spring, 1925: about twenty observed in breeding colony on Isla Raza, Gulf of California (Bancroft, 1932:341, and A. J. van Rossem, personal communication).

19. Spring, 1925: one observed in breeding colony on Isla San Jorge (Georges Island), Gulf of California (van Rossem, personal communication).

20. December 27, 1925: subadult or winter female; North Island Jetty, San Diego, California; Joseph W. Sefton, Jr., SDSNH 10243 (not previously reported). Right wing with two white feathers, left with none (table 1).

21. March 27, 1926: immature male; San Felipe, Baja California (on the Gulf); Raymond Gilmore; MVZ 47843 (not previously reported). (See table 1.)

22. September 12, 1926: subadult or winter male; off Point Loma, San Diego, California; Joseph W. Sefton, Jr.; SDSNH 11237 (not previously reported). Large white patch on each wing (table 1).

23. April 16, 1930: single wing of adult male (fig. 1); Isla Raza, Gulf of California; A. J. van Rossem; DC, UCLA 30170 (not previously reported).

24. February 8, 1948: two observed by authors at Bahía Tortugas, Baja California (p. 221).

25. August 29, 1948: one observed by Robert W. Storer (personal communication); off Golden Gate, California. White patch on each wing.

26. October 15, 1949: two observed by J. R. Pemberton (personal communication); about midway between Ensenada and Islas Todos Santos, Baja California. White patch on each wing.

27. September 24, 1950: one observed by senior author; near Punta Cabras, Baja California (p. 221).

28. November 9, 1950: one observed by junior author; Playa del Rey, California (p. 221).

Table 1

Feathers Involved in White Wing Blotches in Ten Specimens of Heermann Gull

The amount of white in the stated feather of the left and right sides is roughly indicated by 0 = none, 1 = very slight to slight, 2 = moderately small, 3 = medium, 4 = moderately to very large, 5 = complete. The coverts and the primaries are counted from the innermost. Feathers omitted were dark in all specimens examined. The enumeration of the feathers may not be completely precise, because the examination, to avoid damage to the specimns, was rather crude.

	Specimen Numbers (in list on pp. 222–224)										
	1	3	4	5	8	10	16	20	21	22	Average per wing
Greater primary coverts											
3	0–0	0–0	0–0	0–0	0–0	0?–4	0–0	0–0	0–0	0–0	0.0–0.4
4	5–5	3–0	5–0	4–0	0–0	4–5	4–2	0–0	0–2	0–0	2.5–1.4
5	4–5	5–1	4–5	0–1	0–0	5–4	5–5	0–0	3–3	0–4	2.6–2.8
6	4–4	4–5	5–5	0–4	0–3	4–5	4–2	0–0	4–4	4–5	2.9–3.7
7	3–4	4–4	5–0	0–0	0–0	5–4	4–4	0–3	0–0	4–4	2.5–2.3
8	2–5	5–1	5–0	0–0	0–2	4–5	2–5	0–0	3–0	2–2	2.3–2.0
9	4–4	5–1	5–4	0–0	0–0	5–4	1–2	0–4	0–0	5–4	2.5–2.3
10	0–0	2–0	0–0	0–0	0–0	4–0	0–0	0–0	0–0	5–4	1.1–0.4
Avge.	2.7–3.4	3.5–1.5	3.6–1.7	0.5–0.6	0.0–0.6	3.9–3.9	2.5–2.5	0.0–0.9	1.3–1.1	2.5–2.9	2.1–1.9
Primaries											
1	0–0	0–0	3–0	0–0	0–0	1–1	0–0	0–0	0–0	0–0	0.4–0.1
2	0–0	0–0	0–0	0–0	0–0	2–0	0–0	0–0	0–0	0–0	0.2–0.0
3	0–0	0–0	0–0	0–0	0–0	0–4	0–0	0–0	0–0	0–0	0.0–0.4
4	0–0	0–0	0–0	0–0	0–0	4–5	0–0	0–0	0–0	0–0	0.4–0.5
5	0–0	0–0	0–0	0–0	0–0	3–4	0–0	0–0	0–0	0–0	0.3–0.4
6	0–0	0–0	0–0	0–0	0–0	2–2	0–0	0–0	0–0	0–0	0.2–0.2
7	0–0	0–0	0–0	0–0	0–0	3–1	0–0	0–0	0–0	0–0	0.3–0.1
Avge.	2.7–3.4	3.5–1.5	3.6–1.7	0.5–0.6	0.0–0.6	2.1–2.4	0.0–0.0	0.0–0.0	0.0–0.0	0.0–0.0	0.3–0.2

Particularly striking and significant are the consistency of pattern and the essential symmetry of the variants. Except for three specimens which have only two white primary coverts in one wing and no white feathers on the other wing, all variants reported or examined have had a white patch near the bend of each wing. Minor asymmetries have been noted in the size and shape of the patches and in the numbers of feathers variously whitened. Often, white feathers are separated by one or two of normal color. Some greater primary coverts other than the two innermost and the outermost one seem always to be involved, rarely also some secondaries or some primaries, or even some contour feathers on the abdomen (see descriptions and the list above and table 1). The mean number of white coverts per wing is about 4 (table 1).

Occasionally, all defectively pigmented feathers are entirely pure white, or very nearly so, in one or both wings. More commonly, some feathers are piebald, with the dark and light areas either solid, or blotched, or speckled with the opposite shade. In two-toned feathers the dark pigment is usually concentrated along the shaft and near the tip. The degree of whitening of individual feathers grades from a bare trace to completeness (table 1).

The essential consistency and the basic symmetry of the pattern suggest that such aberrations might become segregated, perhaps abruptly, to characterize a new subspecies or species. Speciation along this line would seem to be especially likely in a form such as *Larus heermanni,* which has a relatively limited total population comprising few breeding colonies that occupy only a small proportion of the many available sites. Should the nucleus of a new breeding colony happen to include one of the variants, the aberration might become established rapidly in the expanding population. The "Wright effect" or "drift" might suffice, but the process would be accelerated and be rendered much more probable if the new pattern should have even a slight selectional advantage. Such increases have been observed in the proportion of color variants in certain animals (Huxley, 1943:93-110).

The persistent rarity of the aberration in the Heermann Gull, however, argues against effective selection. As Huxley has indicated in the review just quoted, the proportional numbers of variant types often remain constant over long periods.

The extreme rarily of the variant Heermann Gulls indeed suggests a negative selection. The disadvantage, if any, however, does not seem to involve the social behavior or acceptance of the variants. Their actions and that of their flock companions seem to be approximately normal. At least, unlike some albinos, they are not notably shunned or pecked.

It is possible, however, that the white-marked birds may possess some innate peculiarities of behavior, for plumage mutations appear to be correlated commonly and perhaps characteristically with some distinctive behaviorism, such as tameness (Lee and Keeler, 1951). The mutants seen near Punta Cabras and near Playa del Rey gave evidence of such individuality, for each was among the very last of its flock to be flushed each time it was approached. Such peculiarities in activity might accelerate the organization of plumage mutants into a new race or species.

It may be of significance, from a genetic viewpoint, that among the 21 variants that have been sexed, only 7 were designated as males.

The abnormal white feathering seems to bear almost no relation to the development of the normal white markings of the adult, except in that some birds with unusually large white areas, for example variant number 10 (p. 223) and table 1), appear to have the normal white tip of the secondaries unusually wide and conspicuous. The abnormal white coverts appear in otherwise almost wholly dark juveniles.

Whether all the white-marked variants stem from the breeding grounds on the Gulf islands is not known, for nothing appears to have been determined regarding the presence or absence of the aberration in the population of Isla San Roque, the only breeding station reported on the west side of Baja California (Grinnell, 1928:60). Nor is it known, indeed, whether the breeding populations on the two sides of Baja California intermingle. Even though very rare, such variants may characterize certain populations or even subspecies. Thus, partly black individuals occasionally appear in various parts of the range of the eastern mosquitofish, *Gambusia affinis holbrooki,* but seem to be lacking in the western subspecies, *G. a. affinis.*

No similar color aberration seems to have been reported for any other species of the Laridae, though some color anomalies have been described in the family, as by Robinson (1926) and by Cruickshank (1940). Even in the very similar and apparently closely related species of the Galápagos Islands, namely *Larus fuliginosus,* of which a large series was examined in the California Academy of Sciences, no specimens have been observed with white wing patches. In their general review of the literature on plumage mutants in birds, Lee and Keeler (1951:82) cite only two instances in the family, apparently disregarding the wing-pattern anomaly treated in this paper. Some similar types of variation, but not of identical pattern, have been observed in other birds, for instance in geese (Hanson, 1949).

ACKNOWLEDGMENTS

For data, advise, and use of specimens we are indebted to Alden H. Miller, Museum of Vertebrate Zoology, University of California (MVZ); Robert C. Miller, Robert T. Orr and W. I. Follett, California Academy of Sciences (CAS); Kenneth E. Stager, Los Angeles County Museum (LACM); Thomas R. Howell and the late A. J. van Rossem, Dickey Collection, University of California, Los Angeles (DC, UCLA); James L. Peters, Museum of Comparative Zoology at Harvard College (MCZ); Joseph W. Sefton, Jr., and Lawrence M. Huey, San Diego Society of Natural History (SDSNH); Robert W. Storer and Josselyn Van Tyne, Museum of Zoology, University of Michigan (UMMZ); H. G. Deignan, United States National Museum (USNM); Robert C. Murphy, Charles E. O'Brien and Charles K. Nichols, American Museum of Natural History (AMNH); and J. R. Pemberton, Los Angeles.

SUMMARY

For nearly a century a striking color aberration of the Heermann Gull (*Larus heermanni*) involving a white patch near the bend of each wing, has been reappearing in great rareness, perhaps one in 10,000. In consistency and in symmetry the marking suggests a character to be expected in a related species. Such an aberration might indeed give rise to a new form. The sporadic repetition suggests a recurrent mutation, a homozygous combination, an infrequent phenotypic expression, or an atavistic trait. There is no evidence of strong positive or negative selection. The plumage variants may also have some behavioristic trait, perhaps tameness. The abnormal white feathering bears little relation to the normal development of white areas. Comparable variations are unknown in other gulls.

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Contribution from the Scripps Institution of Oceanography, University of California, La Jolla, California, and *Department of Zoology, University of California, Los Angeles, California, March 1, 1951.*

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Reprinted from
BULLETIN OF MARINE SCIENCE
OF THE GULF AND CARIBBEAN
Vol. 1, No. 3, pp. 149-186
November, 1951

THE NEMERTEAN FAUNAS OF THE GULF OF MEXICO AND OF SOUTHERN FLORIDA

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ABSTRACT

Of the 22 species recorded, 16 were found on the northern Gulf coast and eight in southern Florida. Only two species were common to the two regions. With the exception of two species which appear to be endemic, all those of the northern Gulf coast represent boreal species which occur also on the east coast of North America, although the two faunas have been separated since Pleistocene times by the Florida peninsula. Those of southern Florida are tropical or subtropical forms and some of them are found also in the West Indies or northern South America. The ecological conditions of the northern Gulf coast are so different from those of southern Florida that a more or less complete separation of the littoral invertebrate faunas is not surprising.

The species are treated systematically with a brief description of each, keys for identification, and drawings of the characteristic features.

Nemerteans are found along all the sea-coasts of the world and off the shores to depths of hundreds of meters. Some of the species are circumpolar, extending southward along the Atlantic coasts as far as Madeira or South Africa on the east, and to southern New England or Florida or the Gulf of Mexico on the west, and in the Pacific to California or Mexico on the east and to Japan on the west. A few species live in both the northern and southern hemispheres and a few others in fresh-water streams and lakes. Some are limited to the polar seas and others to the tropics, but many have a wide geographical range and survive under a great variety of environmental conditions. Some of the bathypelagic species live at depths of 1000 to 2000 meters or more and the populations may be carried for thousands of miles by the deep ocean currents, reproducing generation after generation in their endless circuits throughout the great oceans. A few species are parasitic or commensal, while a few others are terrestrial and live beneath

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[1] Contributions from the Scripps Institution of Oceanography, new ser., no. 538.

leaves and other objects in moist situations. More than 700 species have been described but only a few of them have been fully investigated.

NEMERTEAN FAUNAS OF THE GULF OF MEXICO

With the exception of the descriptions of new species, the only report on the nemerteans of the Gulf of Mexico is a brief summary of their geographical distribution published by Coe (1951). That report does not mention the diagnostic features by which the various species may be identified nor their habitat or other ecological peculiarities and these are therefore included in the present paper. The illustrations will aid in species identification. The following account is compiled from collections on the northern coast of the Gulf and from southern Florida. No information is yet available for all those portions of the Gulf coast between Franklin County and Key West, Florida, nor for all that portion of the western Gulf coast south of the Mexican border.

In the areas covered by this report only 16 species have been obtained from the northern Gulf coast and 8 from southern Florida. Only two of these have yet been found in both areas. The presumable explanation for this small number is that only sporadic efforts have been made toward a complete survey of the littoral fauna of those regions. On the Atlantic coast of North America there are 53 known species of nemerteans (Coe, 1943) and on the Pacific coast 95 species (Coe, 1940). Hence, it seems improbable that a very large proportion of all the species now actually living in the Gulf can be included in this report.

Even on the Atlantic coast the nemerteans have been studied extensively only as far south as New Jersey and our knowledge of the species living between that State and Florida is based on collections made at widely separated localities. It may therefore, be assumed that some, perhaps many, additional species remain to be discovered there.

GEOGRAPHICAL DISTRIBUTION. All except two of the species at present known from the northern shores of the Gulf are also found on the Atlantic coast. Therefore, it may be assumed that the nemertean fauna of this part of the Gulf coast has in the geologically recent past been a continuation of that of the Atlantic coast. The present evidence indicates that it is now principally a separate fauna which has been isolated since the last post glacial period in Pleistocene times by the Florida peninsula. To determine to what extent the species of the two areas are at present continuous or overlapping, it is essential to obtain additional collections on both sides of that peninsula. It is already known that some of the species found at Pensacola, on the Gulf side, are identical with those found at St. Augustine, on the Atlantic side. It is now evident that these two nemertean faunas are separated by an area in which other species predominate. Because of the great differences in the environmental conditions between the coasts of northern and southern Florida, a more or less complete separation, but with some overlapping, would seem probable. Only two of the eight species at present known from southern Florida have been found on the northern Gulf coast.

From the small amount of evidence at present available it would appear that the nemerteans on the northern Gulf coast and at St. Augustine, Florida, represent mainly boreal forms, while those at Biscayne Bay and Key West are mostly tropical or subtropical species. In other groups of invertebrates likewise, as well as in fishes, many of the boreal species extend southward along the North Atlantic coast as far as Cape Hatteras or northern Florida and are also found on the northern Gulf coast. The marine fauna of southern Florida, on the other hand, includes species which are identical with those of the West Indies and northern South America. The invertebrate fauna of the northern Gulf coast, however, may contain a mixture of boreal and subtropical species. Deevey (1950) found that the hydroids on the coasts of Louisiana and Texas were dominated numerically by tropical and subtropical forms but that a significant proportion of them were distinctly boreal in distribution.

None of the characteristic boreal and subarctic species of nemerteans of the Atlantic coast, such as *Amphiporus angulatus, A. lactifloreus, A. pulcher, Emplectonema giganteum, Lineus ruber,* or *Cerebratulus marginatus,* have been found in the Gulf. These species do not extend southward along the coast much farther than the Cape Cod region.

Since the coastal water on the west side of the Florida peninsula has a prevailingly northward movement, it is obvious that such of the subtropical species on the southern coast of the Florida peninsula as have free-swimming larvae will tend to be distributed in a corresponding direction until they reach an area in which the conditions in winter are unfavorable for survival.

The nemerteans represent a conservative group and many of the species seem to thrive under a great variety of ecological conditions. As a consequence they often have a wide geographical distribution. Of the 16 species here recorded from the northern Gulf coast, all except *Paranemertes biocellata* and *Amphiporus texanus* are widely distributed on the Atlantic coast and four of them, namely, *Tubulanus pellucidus, Zygeupolia rubens, Zygonemertes virescens* and *Amphiporus cruentatus* occur also on the Pacific coast but not in Europe; two others, *Carcinonemertes carcinophila* and *Tetrastemma vermiculus* are found on European and American Atlantic coasts but not in the Pacific; *Oerstedia dorsalis, Tetrastemma candidum* and *Malacobdella grossa* are circumpolar, inhabiting European shores as well as both the Atlantic and Pacific coasts of North America, while the remaining five species, *Carinoma tremaphoros, Lineus socialis, Micrura leidyi, Cerebratulus lacteus* and *Amphiporus ochraceus* are known only from the Atlantic and Gulf coasts. *Paranemertes biocellata* and *Amphiporus texanus* have been found only on the northern Gulf coast and may possibly represent endemic species.

For comparison, it may be noted that 11 of the 53 species found on the Atlantic coast are identical with species in European waters, while 12 of the Atlantic coast species occur also on the Pacific coast and 2 of these extend also to Japan. No less than 18 of the species found on the Pacific coast are thought to be identical with well-known European species and others are closely similar (Coe, 1943). The nemertean fauna of Bermuda resembles more closely that of Europe and Madeira than that of the American coast in spite of the proximity of the latter.

As a general rule the invertebrates in the Gulf are much smaller when mature than are the members of the same species in more northern and colder localities. This applies likewise to the nemerteans. To anyone familiar with the species on the New England coast, the representatives of the same species in the Gulf appear to be dwarfs. Humes (1942) has described a dwarf variety of *Carcinonemertes carcinophila* from Louisiana, West Indies and eastern South America. Species living among bryozoa, algae and other growths in the intertidal zone farther north are more commonly found beyond the low-tide level in the Gulf. It is evident, however, that relatively few nemerteans live beneath the deeper waters of the Gulf, for the records indicate that only two specimens were obtained during the dredging cruise of the U.S.F.C. Steamer ALBATROSS in 1885. One of these was a species of *Micrura,* while the other represented the genus *Cerebratulus* but they could not be further identified.

REPRODUCTION AND REGENERATION. If ripe individuals of both sexes are available, nearly all these species, but especially *Cerebratulus lacteus,* are suitable for the study of embryological development. From a large ripe female of *C. lacteus* several hundred thousand eggs may be obtained and these usually develop rapidly into pilidium larvae after artificial insemination. Most of the species restore by regeneration the posterior end of the body after injury or removal. *Lineus*

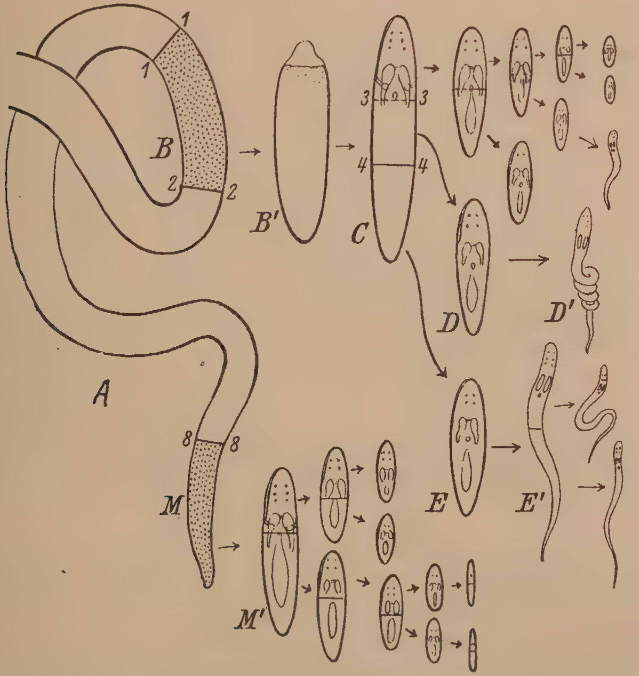

FIGURE 1. Regenerative capacity of body fragments of *Lineus socialis. A,* posterior part of mature worm; *B, C, D, E,* successive regeneration of portions of regenerating fragments when these are cut repeatedly as indicated; *M,* successive regeneration of fragment from posterior end of body.

socialis provides an example of asexual reproduction by fragmentation and is unexcelled for the study of the complete regeneration of minute fragments of the body. Coe (1929-1934) has shown that almost any small piece of the body, provided it contains a portion of one of the nerve cords, will regenerate into a minute replica of the original worm (Figure 1).

Ecology. Most of the species on the Gulf coast are found burrowing in the sand or mud in the low intertidal zone and below to areas where the depth of water is 10 to 20 meters or more. Others live beneath stones or among dead shells, while many of the smaller species occur among bryozoa, algae and other growths in the low intertidal zone and below.

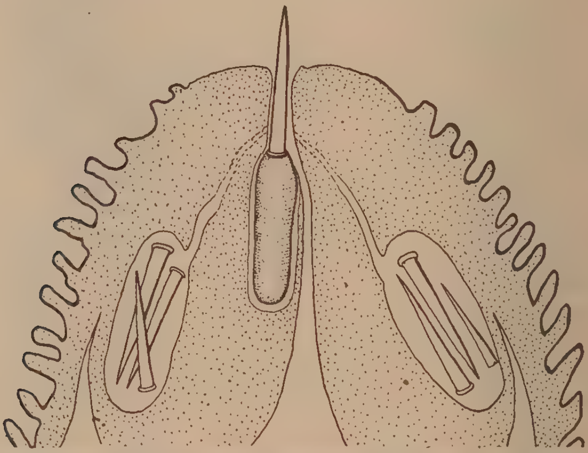

Figure 2. Diagram of fully everted proboscis of *Amphiporus cruentatus*, showing the acutely pointed stylet projecting at the end. The two pouches show newly formed stylets ready for replacement.

Food. Nemerteans are usually carnivorous, feeding on a great variety of worms, crustaceans, mollusks and other small, soft-bodied animals. To secure their prey they are furnished with highly specialized sense organs and most of them with a long, extrusible proboscis. This organ is a formidable weapon, being provided in some species with one or more acutely pointed stylets which puncture and paralyze the prey, allowing the soft parts to be sucked into the mouth (Figure 2). In species without stylets, the proboscis, which is covered with paralyzing and tenacious secretions, can be coiled about the prey, thereby holding it tightly until it can be drawn into the mouth or held until the soft parts can be sucked out.

Because, as has been stated, the nemerteans of the northern Gulf coast are with few exceptions of different species than those found in southern Florida, those of the two areas will be treated in separate sections of this paper.

GEOGRAPHICAL DISTRIBUTION OF SPECIES AT PRESENT KNOWN FROM THE NORTHERN COAST OF THE GULF OF MEXICO

Abbreviations indicate: *A*, Atlantic coast of North America; *E*, coasts of Europe; *G*, northern coast of the Gulf of Mexico; *P*, Pacific coast of North America; *S*, southern Florida; *W*, West Indies; *X*, at other localities.

ORDER PALEONEMERTEA

Tubulanus pellucidus. *A,G,P.*
Carinoma tremaphoros. *A,G.*

ORDER HETERONEMERTEA

Zygeupolia rubens. *A,G.P.*
Lineus socialis. *A,G.*
Lineid sp?
Micrura leidyi. *A,G,S.*
Cerebratulus lacteus. *A,G.*

ORDER HOPLONEMERTEA

Paranemertes biocellata. *G.*
Carcinonemertes carcinophila. *A,E,G.*
Carcinonemertes carcinophila var. imminuta. *G,S,W.*
Oerstedia dorsalis, *A,E,G,P,X.*
Zygonemertes virescens. *A,G,P.*
Amphiporus cruentatus. *A,G,P.*
Amphiporus ochraceus. *A,G.*
Amphiporus texanus. *G.*
Amphiporus sp?
Tetrastemma candidum. *A,E,G, P,X.*
Tetrastemma vermiculus. *A,E,G.*

ORDER BDELLONEMERTEA

Malacobdella grossa. *A,E,G,P.*

GEOGRAPHICAL DISTRIBUTION OF SPECIES FROM SOUTHERN FLORIDA

Abbreviations as in preceding list.

ORDER PALEONEMERTEA

Tubulanus floridanus. *S.*

ORDER HETERONEMERTEA

Baseodiscus delineatus. *E,P,S, W,X.*
Lineus ater. *S,W.*
Lineus stigmatus. *S.*
Micrura leidyi. *A,G,S.*
Cerebratulus fuscus. *E,S,X.*
Cerebratulus leucopsis. *S,W.*

ORDER HOPLONEMERTEA

Carcinonemertes carcinophila var. imminuta. *G,S,W.*
Drepanophorus crassus. *E,P,S, W,X.*

Because of the great differences in the ecological conditions between the coasts of northern and southern Florida, it is not surprising to find a more or less complete separation of the faunas. Only one of the species, *Micrura leidyi,* and the variety *imminuta* of *Carcinonemertes carcinophila* in the foregoing lists have been found in both regions. Hence it would appear that the nemerteans found at St. Augustine and Pensacola represent mainly northern forms, while those at Miami and Key West are principally tropical or subtropical species. In other groups of invertebrates likewise the species found in southern Florida are commonly more closely related with those of the West Indies and northern South America than with the fauna of the Atlantic coast north of Florida.

SECTION I

Key to the species at present known from the northern coast of the Gulf of Mexico, based mainly on easily recognizable external characteristics.

1. With suction disk at posterior end of body; commensal in bivalve mollusks 16
1. Without suction disk; not commensal in bivalves 2
2. Mouth posterior to brain; proboscis not armed with stylete 3
2. Mouth anterior to brain; proboscis with central stylet and in most species with 2 or more pouches of accessory stylets 8
3. Head without lateral longitudinal grooves 4
3. Head with lateral longitudinal grooves 6
4. Posterior end without slender caudal cirrus 5
4. Posterior end with long caudal cirrus; head acutely pointed *Zygeupolia rubens*
5. Body small, white; posterior end slender .... *Tubulanus pellucidus*
5. Body when mature usually 30-150 mm long; red or yellowish red; posterior end broad and flattened .... *Carinoma tremaphoros*
6. Body slender, rounded; head with 2 to 8 pairs small ocelli .. *Lineus socialis*
6. Body flattened in intestinal region; head without ocelli 7
7. Lateral margins rounded in intestinal region; not adapted for swimming; color dark red .... *Micrura leidyi*

7. Lateral margins in intestinal region thin; adapted for swimming; color white, pale yellow or rosy .... *Cerebratulus lacteus*
8. Proboscis with central stylet only and no accessory stylets; parasitic on crabs .... *Carcinonemertes carcinophila*
8. With 2 or more pouches of accessory stylets; not parasitic 9
9. Proboscis with 4 or 8 pouches of accessory stylets; only one pair of ocelli *Paranemertes biocellata*
9. Proboscis with only 2 pouches of accessory stylets; head with more than one pair of ocelli 10
10. Ocelli numerous, extending posteriorly beyond head *Zygonemertes virescens*
10. Ocelli limited to head 11
11. More than 2 pairs of ocelli 12
11. Only 2 pairs of ocelli 14
12. Ocelli in a single row on each side of head; blood corpuscles red *Amphiporus cruentatus*
12. Ocelli in several groups or irregular rows; blood nearly colorless 13
13. Central stylet of proboscis rounded at both ends and slightly constricted in the middle .... *Amphiporus ochraceus*
13. Central stylet truncated at both ends; not constricted in the middle *Amphiporus texanus*
14. Yellowish, without spots of dark pigment .... *Tetrastemma candidum*
14. Body small, cylindrical; color variable; irregularly spotted with brown.. 15
15. Body short and firm; ocelli large, those of the same side not connected by band of pigment .... *Oerstedia dorsalis*
15. Body soft, yellowish; the two ocelli of same side connected by band of dark pigment .... *Tetrastemma vermiculus*
16. Body with suction disk at posterior end; commensal in bivalve mollusks *Malacobdella grossa*

Systematic Descriptions of Species

The following abbreviated descriptions of the species at present known from the northern coast of the Gulf are based mainly on easily recognizable external characteristics. The geographical range as given indicates the limits of the species in so far as at present known and should not be interpreted as implying that the species will not later be found elsewhere.

Order 1, PALEONEMERTEA

Family Tubulanidae

Tubulanus pellucidus Coe, 1940, 1943

Carinella pellucida Coe, 1895.

The minute worms belonging to this species may be recognized by their soft, slender, white bodies and by the absence of both ocelli and longitudinal grooves on the head (Figure 3). Length when mature 10 to 25 mm, width 1 mm or less.

The worms live in delicate cellophane-like tubes among algae and

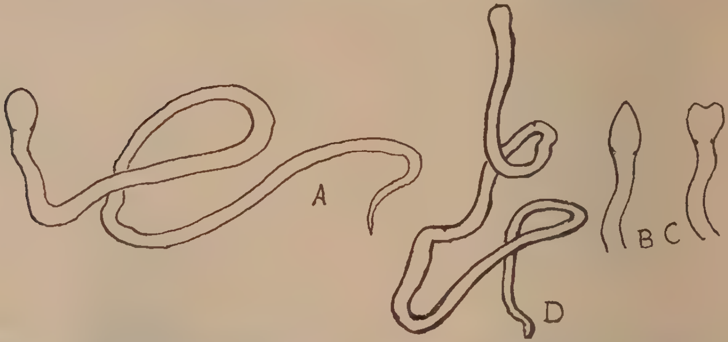

FIGURE 3. *Tubulanus pellucidus. A, D,* outlines of body; *B, C,* anterior ends in different states of contraction.

other growths in the intertidal zone and below to a depth of at least 20 meters. Recorded from southern New England to northern Florida on the Atlantic coast and has been found also at Pensacola, Florida, on the Gulf coast. It presumably occurs elsewhere along the Gulf coast. Found also from Monterey Bay to San Diego, California.

Family CARINOMIDAE

CARINOMA TREMAPHOROS Thompson, 1900; Coe, 1943

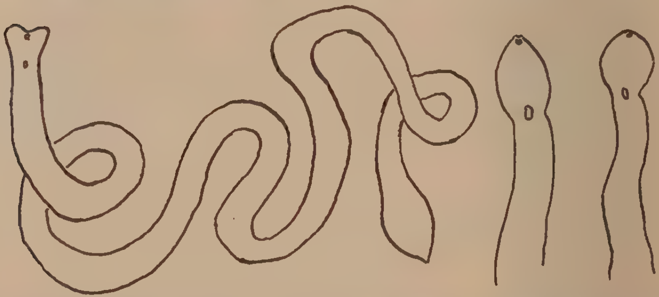

FIGURE 4. *Carinoma tremaphoros.* Outlines showing variations in shape of head in different states of contraction and the broad and flat posterior extremity of body.

Body pale reddish or yellowish, with broadened posterior end, which is without caudal cirrus. Head broad, without ocelli or longitudinal grooves (Figure 4). Length when mature 30 to 150 mm, width 2 to 5 mm. The worms burrow in mud, sandy mud and clay or live beneath stones in the intertidal zone and below from Cape Cod to northern Florida and on the Gulf coast at least as far west as Louisiana.

Order 2, HETERONEMERTEA

Family LINEIDAE

ZYGEUPOLIA RUBENS Coe, 1905, 1940, 1943

Valencinia rubens Coe, 1895; *Zygeupolia litoralis* Thompson, 1900.

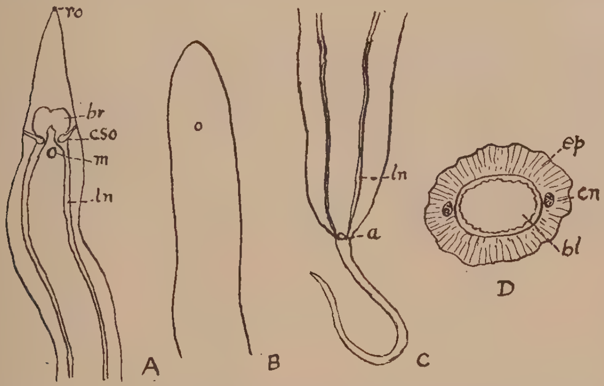

FIGURE 5. *Zygeupolia rubens. A, B,* diagrams of anterior portions of body of two individuals, one of which is extended and the other contracted. *C,* posterior end of body, showing long caudal cirrus with central blood space. *D,* transverse section of caudal cirrus, showing central blood space (*bl*), pair of caudal nerves (*cn*) and outer ciliated epithelium (*ep*). Other letters indicate: *a,* anus; *br,* brain; *cso,* cerebral sense organ; *ln,* lateral nerve cord; *m,* mouth; *ro,* rhynchodeal opening.

The worms of this species may be identified by the red or rosy color, sharply pointed head and long caudal cirrus (Figure 5). The head is white and usually sharply pointed in life but is rounded when strongly contracted. There are no ocelli or longitudinal grooves. Length 40 to 80 mm when mature; width 2 to 5 mm.

Found in sand or beneath stones in the intertidal zone and below from southern New England to northern Florida and on the Gulf coast westward to Copano Bay, Texas.

LINEUS SOCIALIS Verrill, 1892; Coe, 1943

Nemertes socialis Leidy, 1855.

Recognized by the very slender body, with a row of 4 to 8 small ocelli on each side of head (Figure 9) and by the tendency of the

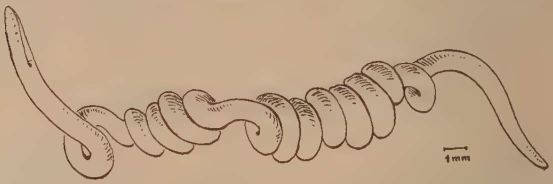

Figure 6. *Lineus socialis;* outline of body, showing coiled condition when strongly contracted.

worms to coil in spiral when disturbed (Figure 6). Length when mature 30 to 150 mm, width 1 to 3 mm. Color variable, often pale olive green, greenish brown or reddish brown; frontal margin and lateral borders of head whitish; brain region bright red; body sometimes encircled with 6 to 20 or more narrow and inconspicuous rings of lighter color.

These little worms live beneath stones and among mussels and other growths in the intertidal zone from Bay of Fundy to northern

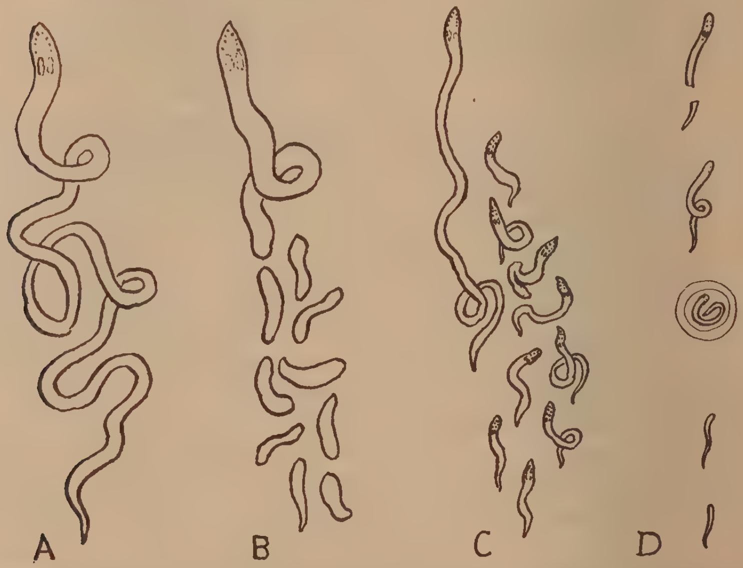

Figure 7. *Lineus socialis*. Diagram of asexual reproduction by natural fragmentation. *A*, mature worm; *B*, same after producing nine fragments; *C*, regeneration of each fragment, resulting in ten smaller worms of normal proportions; *D*, regeneration of minute fragments cut from body of regenerating fragment; one of these has formed a temporary cyst.

Florida and on the Gulf coast westward to Texas. Locally common and often gregarious.

This species differs from all others on this coast by its capacity for asexual reproduction by fragmentation (Figure 7). If the body be cut into many small pieces, each fragment will ordinarily regenerate into a minute replica of the original worm (Figure 1). Temporary encystment of small regenerating fragments often occurs (Figure 7). For complete regeneration the fragment must contain a portion of at least one of the nerve cords. This is excellent material for such studies, since the worms or their fragments may live for a year or more in jars of sea-water with pebbles in the bottom, provided the water be changed occasionally (Coe, 1929-1934). Furthermore various types of twinning may be produced by splitting a regenerating fragment at one or both ends. The twinned individuals eventually separate into two or more complete worms (Figure 8). A period of asexual reproduction may be followed by dioecious sexual reproduction in which the sexes mate and the eggs are deposited in a thick mucous sheath.

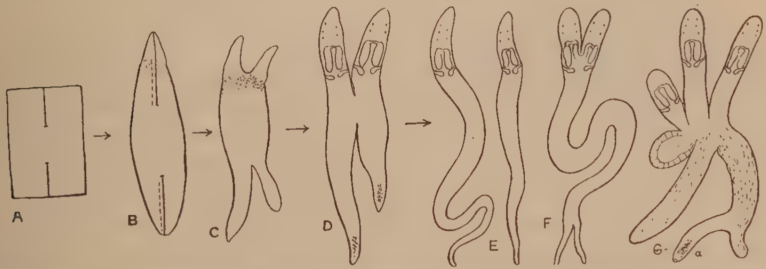

FIGURE 8. *Lineus socialis.* Twins produced by splitting regenerating fragment at both ends.

The nephridial system, which has not been fully described heretofore, is peculiar in being divided into a short anterior portion on each side, separated by the mouth and anterior esophageal region from the more extensive posterior system. The anterior portion is limited to the short space on the lateral wall of the cephalic blood lacuna between the cerebral sense organ and the mouth. Here a comparatively large longitudinal canal lies in a narrow ridge on the wall of each of the lacunae and is thereby almost entirely surrounded by the blood (Figure 9). From the longitudinal canal the efferent duct leads to the

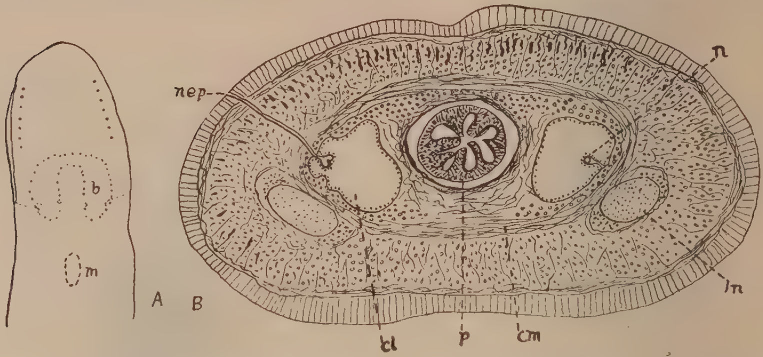

FIGURE 9. *Lineus socialis. A,* outline of head, showing position of the 7 pairs of ocelli, brain (*b*) and mouth (*m*). *B,* transverse section of head between brain and mouth, showing anterior pair of nephridial canals (*n*) projecting freely in lumens of cephalic blood lacunae (*cl*), with one of the pair of efferent nephridial ducts (*nep*) opening on the dorsolateral aspect of the head. Other letters indicate: *cm,* circular musculature; *ln,* lateral nerve cord; *p,* proboscis.

dorsolateral surface of the head posterior to the cephalic groove. In each of two specimens sectioned the efferent duct on the left side was near the posterior end of the longitudinal canal and that on the right side near the anterior end. A small number of flagellated terminal cells lie in the connective tissue bordering the lacunae.

The posterior portion of the nephridial system on each side is much more extensive and consists of a long, convoluted tubule in the usual position beside almost the entire length of the fore gut, with a multitude of terminal cells and several efferent ducts leading to the dorsolateral surfaces of the body.

In several other species of *Lineus,* notably *L. geniculatus* (D. Chiaje), *L. lacteus* Grube and *L. nigricans* Bürger, as well as in certain species of *Cerebratulus,* the nephridia likewise extend forward in ridges on the walls of the cephalic lacunae but in these cases the entire system on each side of the body is connected.

MICRURA LEIDYI (Verrill)

Meckelia rosea Leidy, 1851; *Cerebratulus leidyi* Verrill, 1892; *Micrura leidyi,* Coe, 1943.

This is one of the most common of the species of ribbon worms in the Gulf and along the east coast of the United States. The body

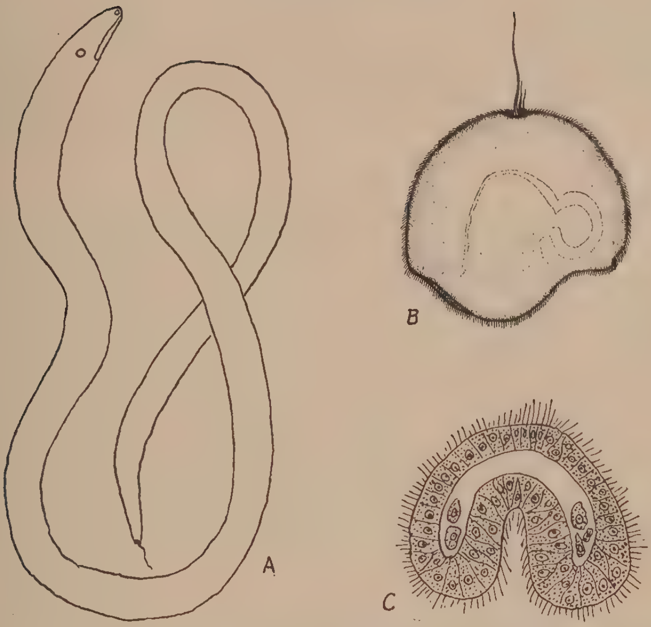

FIGURE 10. *Micrura leidyi. A,* outline of body, showing mouth, rhynchodeal opening and one of the cephalic grooves. *B,* early pilidium, with ciliated esophagus and primitive intestine. *C,* gastrula, with mesenchyme cells in cavity.

is rather slender, cylindrical in anterior portion and much flattened in intestinal region; very fragile; head slender, without ocelli; mouth small, caudal cirrus small (Figure 10).

Color deep red or purplish red, lighter anteriorly; anterior border of head and mouth region whitish. Length 20 to 200 mm, width 1 to 6 mm.

Lives in sand, sandy mud and under stones in the intertidal zone and in shallow water from Massachusetts Bay to the coast of northern Florida and in the Gulf at least as far west as Texas. In some localities on the northern Gulf coast it is more abundant than any other species of nemertean.

Individuals of this species are among the most fragile of all nemerteans and usually break into many pieces when lifted from the sand. The numerous eggs, which are excellent for embryological studies, are shed into the water from July to October on the coast of southern

New England, but the season of reproduction in the Gulf is not at present known. The larvae can be reared to the pilidium stage without difficulty (Figure 10). The adult worms have the capacity for the rapid posterior regeneration of fragments from the anterior part of the body but if the head be removed it is seldom, if ever, restored.

MICRURA sp?

One specimen which the writer is unable to identify as belonging to any described species was dredged in 1885 at Station 2400 in the Gulf of Mexico at 28°41′ N. Lat., 86°07′ W. Long, in gray mud at a depth of about 510 meters. This locality is far offshore south of Cape San Blas.

The head is slender and rather sharply pointed anteriorly, with long cephalic grooves and is peculiar in having the rhynchodeal opening on the ventral surface some distance posterior to the tip of the head. The mouth is a small oval slit. The posterior end of the body is missing, but the fragments of the body that remain measure about 40 mm in length and 2 to 3 mm in width. The preservation is not satisfactory for microscopical study and the color remaining is uniformly brown.

CEREBRATULUS LACTEUS Verrill, 1892; Coe, 1943

Mecklia lactea Leidy, 1851; *M. ingens* Verrill, 1873.

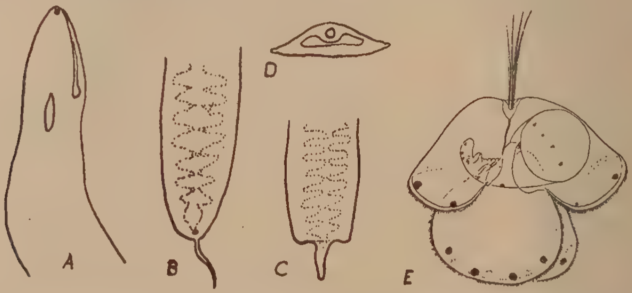

FIGURE 11. *Cerebratulus lacteus. A,* anterior end of body, showing the large mouth, subterminal rhynchodeal opening and one of the long cephalic grooves; *B,* posterior end with caudal cirrus; *C,* regeneration of posterior end of body; *D,* tranverse section through intestinal region, showing thin lateral margins; *E,* pilidium larva. (*E,* after Verrill.)

The body is long and ribbon-like, with flattened intestinal region and thin lateral margins; well adapted for swimming. Ocelli absent; caudal cirrus slender (Figure 11).

Mature individuals are larger than any of the other nemerteans at present known on the Gulf coast, often exceeding a meter in length. Color variable; whitish, pale yellow, flesh color, pale red or salmon. Young individuals are usually translucent white or pale yellow, with brown intestinal diverticula.

This is a common species, burrowing in the mud or sand in the intertidal zone from Maine to northern Florida and along the Gulf coast to Port Aransas, Texas.

Each large female produces each season many thousand translucent ova which are fertilized in the water and develop rapidly into pilidium larvae (Figure 11). The eggs of this species have been widely used in experimental studies and for class demonstrations. Posterior regeneration takes place readily but anterior regeneration is limited to the head anterior to the brain. With occasional changes of the sea-water and low temperature, a worm of this species, with or without head, may live for several months without food, the body meanwhile being reduced to a small fraction of its original size.

Order 3, HOPLONEMERTEA

Family EMPLECTONEMERTIDAE

PARANEMERTES BIOCELLATA Coe, 1944

This species may be recognized by the slender body, with sharply pointed head bearing a single pair of oval, black ocelli near the tip. The color of the body is pale green with a slightly rosy tinge. The proboscis is provided with a slender central stylet about two-thirds as long as the slender, cylindrical basis. There are either four or eight pouches of accessory stylets and 12 proboscidial nerves. Size when mature 60 to 120 mm in length and 2 to 4 mm in width. Details of organ systems are shown in Figure 12.

This species is at present known only from Biloxi, Mississippi, where it has been found burrowing in the intertidal sand flats and in shallow water.

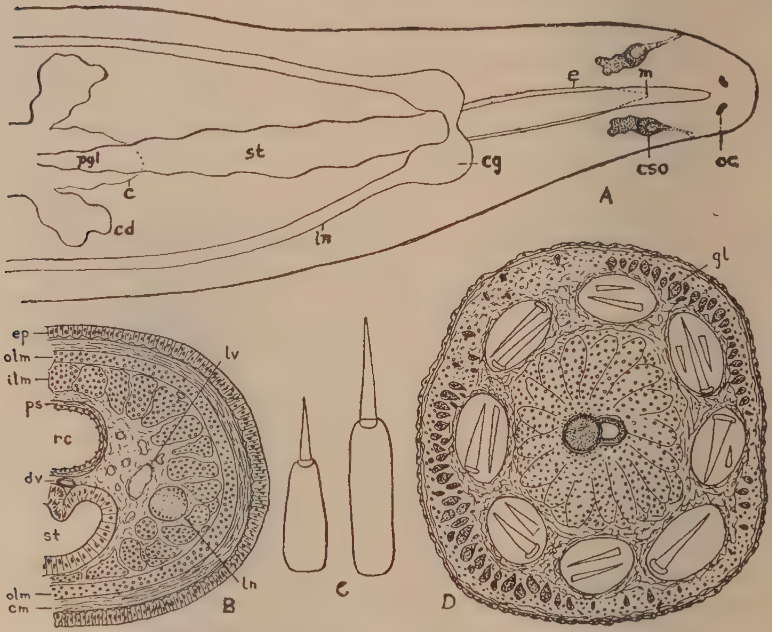

FIGURE 12. *Paranemertes biocellata. A,* diagram of organ systems in anterior end of body; *c,* caecum; *cd,* caecal diverticulum; *cg,* cerebral ganglion; *cso,* cerebral sense organ; *e.* esophagus; *ln,* lateral nerve cord; *m,* opening of mouth into rhynchodeum; *oc,* ocellus; *pyl,* pylorus; *st,* stomach. *B,* portion of transverse section of body posterior to brain, showing the two layers of longitudinal muscles; *cm,* circular muscular layer; *dv,* dorsal blood vessel; *ep,* epithelium of body wall; *ilm,* inner layer of longitudinal muscles; *ln,* lateral nerve cord; *lv,* lateral blood vessel; *olm,* outer layer of longitudinal muscles; *ps,* proboscis sheath; *rc,* rhynchocoel; *st,* stomach. *C,* central stylet and basis from two individuals. *D,* diagram of transverse section through septum of proboscis, showing, in center, stylet basis and canal leading from anterior to posterior proboscis chamber, and longitudinal musculature surrounded by eight pouches of accessory stylets; *gl,* wreath of pigmented gland cells.

Family CARCINONEMERTIDAE

CARCINONEMERTES CARCINOPHILA Coe, 1902

Nemertes carcinophilon Kolliker, 1845; *C. carcinophila* Humes, 1941, 1942.

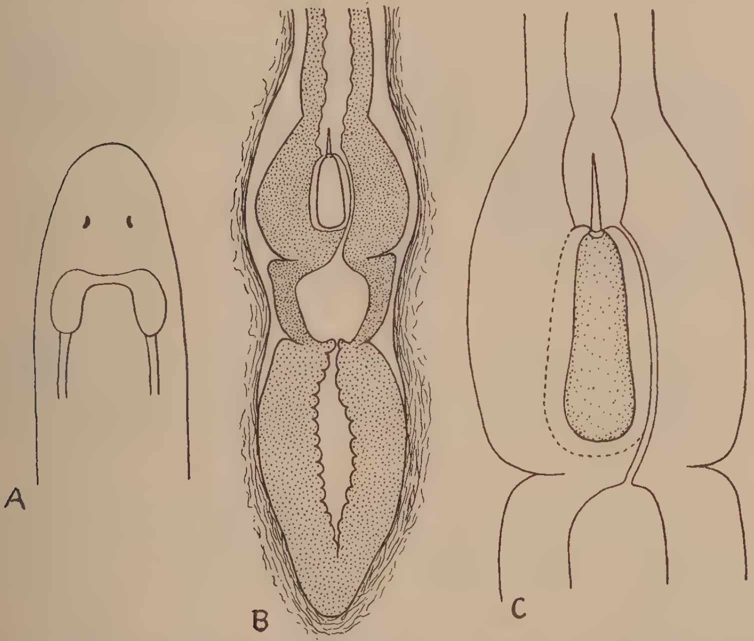

FIGURE 13. *Carcinonemertes carcinophila. A,* outline of head, showing brain and ocelli. *B,* proboscis, with posterior chamber immovably attached to proboscis sheath. *C,* middle portion of proboscis with stylet on elongated basis and canal leading from anterior to posterior chamber.

These curious little nemerteans are parasitic on the gills of various species of crabs when young and during the season when the crabs are without eggs. They migrate to the egg-masses of the host as soon as these are produced. Reproduction occurs only when on the egg-masses.

The slender body, 20-70 mm in length, is colored in various shades of red; there is a single pair of ocelli on the head. The proboscis is very short and can be extended only as far as the tip of the head; it has a slender central stylet and basis but no accessory stylets (Figure 13).

In this genus the sexes are separate, the numerous ovaries being of the usual hoplonemertean type, while the male reproductive organs differ from those known for any other nemerteans. The numerous spermaries connect with a single longitudinal spermatic duct which opens into the posterior portion of the rectum (Figure 14). At the time of reproduction a male and a female place their bodies side by side and secrete a thick sheath of mucus in which a hundred or more relatively large eggs are deposited. Development is of the direct type. The morphology and biology of this species are fully described by Humes (1942).

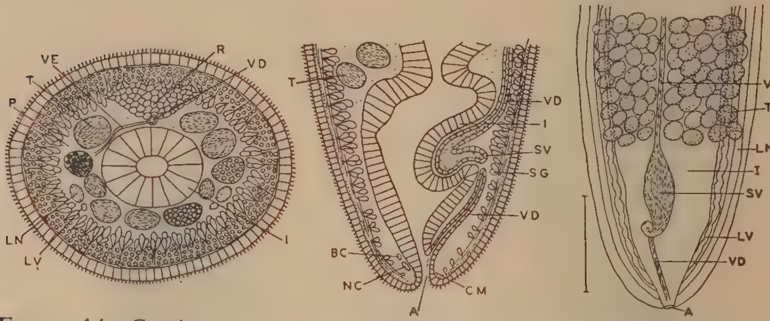

FIGURE 14. *Carcinonemertes carcinophila.* Diagrams of transverse and longitudinal sections of body of male, showing the numerous spermaries (*T*), with seminal vesicle (*SV*) and common efferent duct (*VD*) opening into the intestine near the anus (*A*). Other letters indicate: *I*, intestine; *LN*, lateral nerve cord; *LV*, lateral blood vessel; *SG* submuscular glands. (From Humes, 1942).

Crabs of the family Portunidae, particularly the lady crab (*Ovalipes ocellatus*) and the blue crab (*Callinectes sapidus*) on the American Atlantic coast and *Carcinides maenas* in European waters are most frequently infested. On the Gulf coast *Callinectes sapidus* is the usual host but representatives of other families are occasionally infested (Humes, 1942). With the needle-like central stylet the young worms presumably puncture the gills of the host and suck out the blood, while the adults similarly puncture the eggs of the host and devour the contents, whether yolk or embryo. It seems probable that additional food for both young and adult is obtained from such small animals as may be encountered.

Found on the Atlantic coast from the Bay of Fundy to Florida and along the Gulf coast to Texas, as well as on European shores from Scotland to the Mediterranean.

CARCINONEMERTES CARCINOPHILA, var. IMMINUTA Humes, 1941, 1942

This variety differs from the typical form in being of smaller size when mature, in having a shorter and more slender stylet basis, a shorter stylet and in other minor morphological details. This variety was more abundant on *Callinectes sapidus* than on any other crabs at Grand Isle, Louisiana, and on other species in the West Indies, Panama and Brazil.

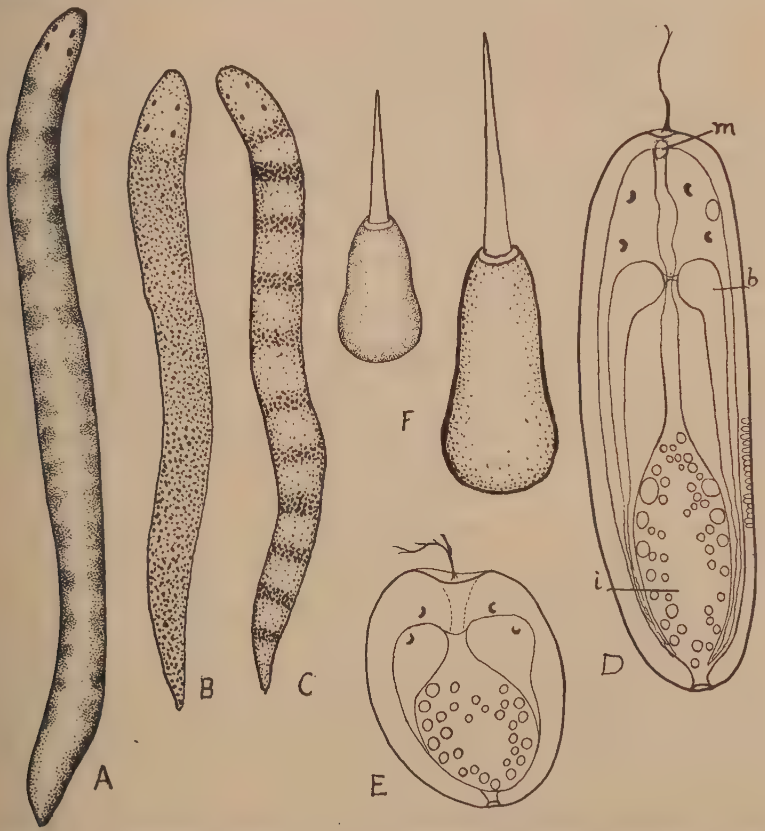

FIGURE 15. *Oerstedia dorsalis. A, B, C,* three of the many variations in color patterns; *D,* embryo with direct type of development, showing mouth (*m*), intestine (*i*), brain (*b*), and the four large ocelli; *E,* same when contracted; *F,* variations in size of central stylet and basis in small and large individuals.

Family PROSORHOCHMIDAE

OERSTEDIA DORSALIS Bürger, 1895; Coe, 1940, 1943

Planaria dorsalis Abildgaard, 1806; *Tetrastemma dorsale* Verrill, 1892.

Individuals of this widely distributed species may be recognized by their small cylindrical, firm bodies, often brightly colored and spotted or banded in conformity with their environment. They have a superficial resemblance to species of *Tetrastemma* and the same number of ocelli but the body is relatively shorter, firmer and less flattened. They are also less active in their movements.

Mature individuals seldom exceed 10 to 20 mm in length and 1 to 2 mm in diameter. The head bears 4 rather conspicuous ocelli. Proboscis relatively large; provided with slender stylet on pear-shaped basis and 2 pouches of accessory stylets (Figure 15.) The colors are extremely variable, with shades of red, brown, olive, whitish or yellowish and spotted, banded or striped with more deeply colored pigment (Figure 15).

Locally abundant among algae, bryozoa and other growths on rocks and piles in the low intertidal zone and below on the coasts of Europe to Madeira; on the Atlantic coast of North America from Nova Scotia to northern Florida; on the Gulf coast westward to Texas; and on the Pacific coast from Puget Sound to Mexico. The relatively large eggs undergo the direct method of development (Figure 15).

Family AMPHIPORIDAE

ZYGONEMERTES VIRESCENS Montgomery, 1897; Coe, 1940, 1943

Amphiporus virescens Verrill, 1879, 1892; *Ophionemertes agilis* Verrill, 1873; *Amphiporus agilis* Verrill, 1892.

The slender, cylindrical, greenish worms belonging to this species differ from all others known from the region in having very numerous minute ocelli which extend along the sides of the body far posterior to the brain (Figure 16). Living individuals may also be distinguished from those of other species by their restless, rapid movements. The proboscis sheath extends the entire length of body and the proboscis is armed with a slender central stylet with massive basis truncated posteriorly (Figure 16) and with 2 lateral pouches usually containing 3 accessory stylets each. Length of body when mature 10 to 40 mm, width 1 to 2 mm.

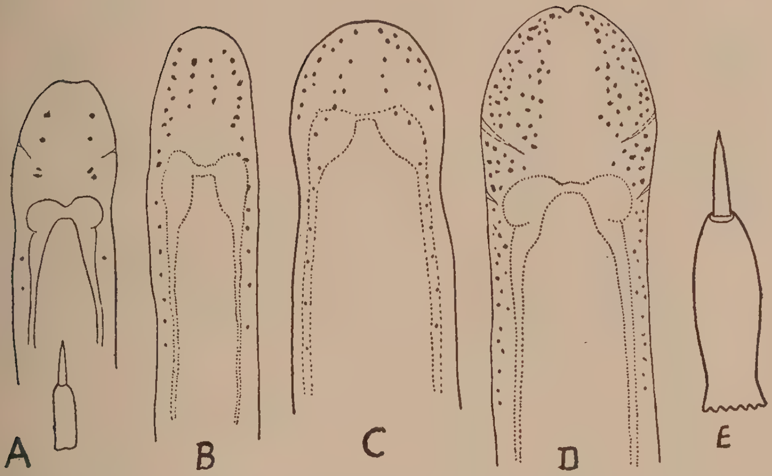

FIGURE 16. *Zygonemertes virescens.* Variations in the number and arrangement of ocelli and in size of central stylet and basis in young and older individuals; the stylet basis in *A* and *E* are drawn at the same scale of magnification.

The species is locally common among algae, bryozoa and other growths on rocks and other objects in the low intertidal zone and below. It occurs from the Bay of Fundy to northern Florida and along the Gulf coast at least as far as Pensacola, Florida. It is also found on the Pacific coast from British Columbia to Mexico.

AMPHIPORUS CRUENTATUS Verrill, 1879; Coe 1940, 1943
Amphiporus leptacanthus Coe, 1905.

Individuals of this species are easily recognized in life by their pale yellow color, with three slender longitudinal red lines representing the longitudinal blood vessels, as well as by the single row of 5 to 10 ocelli on each side of the head (Figure 17). Central stylet of proboscis long and slender, on long, slender basis (Figure 2, 17). Length when mature 10 to 30 mm, width 1 to 4 mm. Blood corpuscles bright red.

Lives among algae, bryozoa and other growths on rocks and beneath stones and shells in the intertidal zone and below from New England to northern Florida and on the Gulf coast at least as far as Pensacola, Florida, as well as on the Pacific coast from Puget Sound to Mexico.

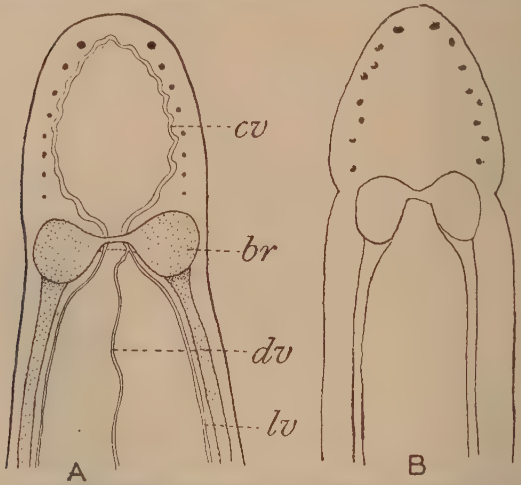

FIGURE 17. *Amphiporus cruentatus. A,* diagram of anterior end of body, showing brain (*br*), cephalic (*cv*), dorsal (*dv*) and lateral (*lv*) blood vessels and arrangement of ocelli; *B,* head with larger ocelli; *C,* variations in central stylets and bases.

This is a good species for the study of posterior regeneration, the restoration of a lost proboscis, and the reorganization of fragments cut from the anterior portion of the body.

AMPHIPORUS OCHRACEUS Verrill, 1892; Coe, 1943

Cosmocephala ochracea Verrill, 1873; *A. greemani* Montgomery, 1897.

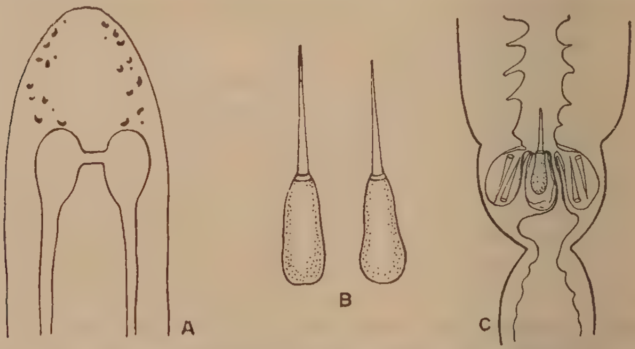

FIGURE 18. *Amphiporus ochraceus. A,* outline of head, showing arrangement of ocelli; *B,* central stylets and bases; *C,* middle chamber of proboscis, with armature.

In this species the body is slender and yellow, whitish or grayish in color, sometimes with tinge of orange anteriorly and occasionally with brown intestinal diverticula. The length when mature varies from 10 to 70 mm and the width 1 to 3 mm. The head bears 6 to 14 small ocelli in irregular rows on each lateral margin, bending medially toward the brain (Figure 18). The proboscis has a slender central stylet and basis, with usually two accessory stylets in each of the two pouches (Figure 18).

Locally common beneath stones and among algae and other growths in the intertidal zone and below from Massachusetts Bay to Florida and in the Gulf westward to Port Aransas, Texas.

AMPHIPORUS TEXANUS Coe, 1951

This species represents one of the larger and broader forms of this extensive genus. The type specimen was about 60 mm in length and 6 mm in width after preservation. The length of this specimen is therefore only 10 times the greatest width. The head is narrow, about 2 mm in width, with subterminal mouth and transverse or oblique lateral

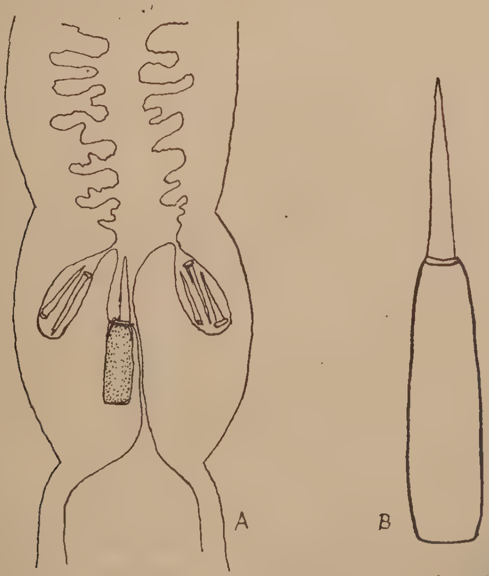

FIGURE 19. *Amphiporus texanus. A,* middle chamber of proboscis, with armature; *B,* central stylet and basis.

grooves. There are many small ocelli on each side of the head, although the exact number and arrangement have not been determined.

The proboscis is large and extends nearly the entire length of the body. The central stylet is moderately slender and about two-thirds as long as the relatively massive basis. The latter is nearly rectangular in outline, about four times as long as its diameter, tapering but slightly toward the anterior end and is truncated posteriorly (Figure 19.) There are two pouches of accessory stylets and 10 rather large proboscidial nerves.

No record is available regarding the color in life, but the specimen preserved in formalin indicated a pale, reddish brown epidermal pigmentation.

The cerebral sense organs are comparatively larger than in most species of the genus. They are situated lateroventrally and a short distance anterior to the brain.

At present known only from the type specimen which was collected at Port Aransas, Texas.

AMPHIPORUS sp?

Among the nemerteans collected by Don Carpenter at Alligator Bay, Franklin County, Florida, was one specimen of a species of *Amphiporus* which apparently represents an undescribed species but for which no satisfactory diagnosis can now be supplied because of the absence of the proboscis.

The body is fusiform and moderately slender, measuring after preservation 18 mm in length and 2 to 3 mm in width. The color after preservation is milk white. The head is provided with a row of 10 remarkably large ocelli on each lateral border and a group of 5 smaller ocelli on each side situated more posteriorly and nearer the median line. Mouth and rhynchodeal opening in close contact. Cerebral sense organs large, situated beside and behind brain with large canals to lateral borders of head.

Family TETRASTEMMATIDAE

TETRASTEMMA CANDIDUM McIntosh, 1873, Verrill, 1892; Coe, 1940, 1943

Fasciola candida Müller, 1774.

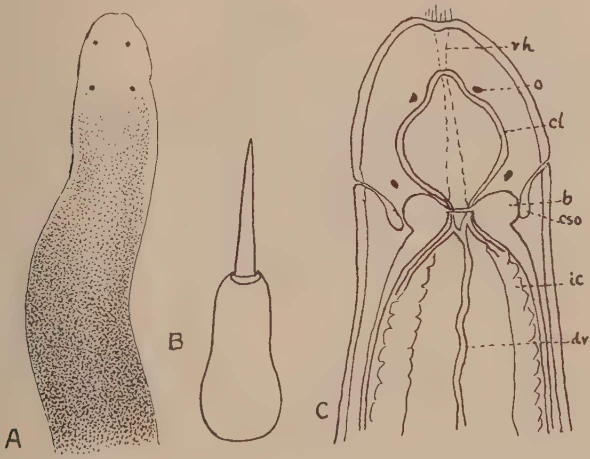

FIGURE 20. *Tetrastemma candidum. A,* anterior end of body, showing ocelli and pigmentation; *B,* central stylet and basis; *C,* diagram of organ systems; *b,* brain; *cso,* cerebral sense organ; *cl,* cephalic lacuna; *dv,* dorsal blood vessel; *ic,* intestinal caecum; *o,* ocellus; *rh,* rhynchodeum.

These little worms (Figure 20) may be identified by the pale green or yellowish green body without markings. Young individuals are pale yellow laterally and green medially. There are 2 pairs of conspicuous reddish brown ocelli anterior to the brain (Figure 20). The stylet basis is rounded at both ends and slightly enlarged posteriorly (Figure 20). Length of the body when mature 10 to 20 mm, occasionally 35 mm; width 0.5 to 1.5 mm.

Locally common among bryozoa, algae and other growths in the intertidal zone and below from Labrador to northern Florida and on the Gulf coast at least as far west as Louisiana. Found also on European coasts, Madeira and South Africa, as well as on the Pacific coast from Alaska to Mexico. This is a typical circumpolar species.

TETRASTEMMA VERMICULUS Stimpson, 1857; Verrill, 1892; Coe, 1943

Polia vermiculus Quatr., 1846.

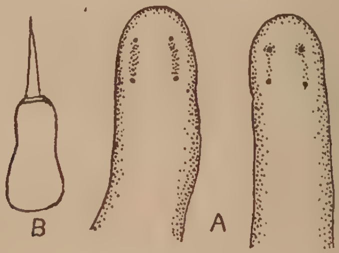

FIGURE 21. *Tetrastemma vermiculus. A,* outlines of the heads of two individuals, showing variations in the width of the longitudinal band of pigment connecting the two ocelli of the same side. *B,* central stylet and basis.

This species resembles *T. candidum* in many respects but differs in having a whitish, light yellow or pale reddish body and in having the two ocelli of the same side conected by a narrow band of dark pigment (Figure 21). A narrow ring of pigment often surrounds the anterior ocelli. The body is slender and seldom more than 15 to 20 mm long and 1 mm wide.

The proboscis is longer than the body and is provided with a relatively large basis somewhat constricted near the middle and slightly longer than the stylet (Figure 21). There are two pouches of accessory stylets and ten proboscidial nerves. The cerebral sense organs are relatively large and are situated anteroventrally to the brain.

Locally common among algae and bryozoa in the intertidal zone and below from the Bay of Fundy to northern Florida and on the Gulf coast westward to Texas. Found also on European coasts from Norway to Madeira.

Order 4, BDELLONEMERTEA

Family MALACOBDELLIDAE

MALACOBDELLA GROSSA (O. F. Müller), 1776

M. grossa Bürger, 1895; Gering, 1911; Riepen, 1933; Coe, 1940; *M. obesa, M. mercenaria* Verrill, 1892.

Body short and broad, wider at posterior end which bears a comparatively large suction disk (Figure 22).

Length when mature 20 to 40 mm, width 8 to 15 mm. Color white, gray, pale yellow or brownish. Ocelli and cerebral sense organs absent. Alimentary canal narrow, cylindrical and convoluted; without diverti-

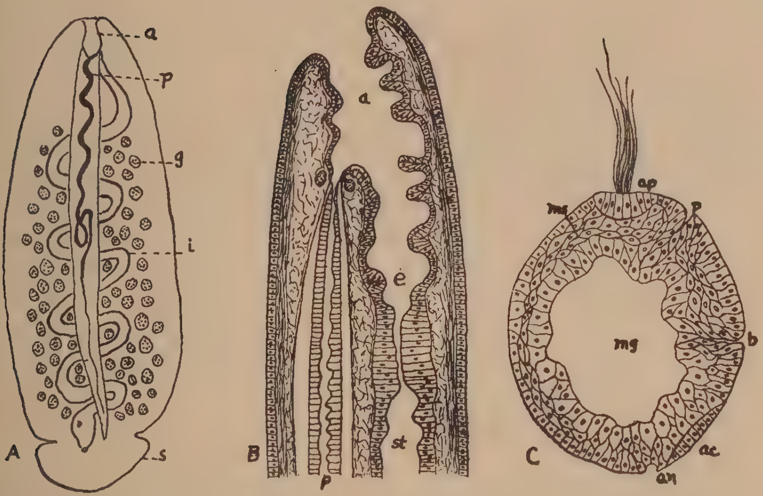

FIGURE 22. *Malacobdella grossa. A,* outline of internal organs; *a,* atrium; *g,* one of the numerous gonads; *i,* convoluted intestine, with rectum and anus at base of suction disk; *p,* proboscis in proboscis sheath; *s,* suction disk. *B,* sagittal section through anterior end of body, showing atrium (*a*), esophagus (*e*), stomach (*st*) and attachment of phoboscis (*p*). *C,* larva with apical tuft of flagella (*ap*), invaginating proboscis (*p*), blastopore (*b*), midgut (*mg*), anus (*an*) and primordium of suction disk (*ac*). (*C,* after Hammersten.)

cula (Figure 22). Proboscis slender, with weak musculature and without stylets. Gonads in both sexes small and numerous. Eggs that are artificially fertilized develop rapidly without metamorphosis (Figure 22).

Commensal in the mantle cavity of various species of bivalve mollusks; on the Atlantic and Gulf coasts more commonly in *Venus mercenaria* than in any other species. Widely distributed on European shores as far south as the Mediterranean; on the American Atlantic coast from Nova Scotia to Florida, on the Gulf coast westward to Texas and on the Pacific coast as far south as California. It probably causes little, if any, injury to the host, since it feeds mainly on the larger particles which the mollusk draws into its mantle cavity but does not ingest.

SECTION 2.

Key to species at present known from southern Florida

1. Proboscis without stylets, mouth posterior brain 2
1. Proboscis with one or more stylets; mouth anterior to brain 8
2. Head with a pair of lateral longitudinal grooves 4
2. Head without longitudinal grooves 3
3. Body brown, encircled by many rings of lighter color; lateral nerve cords external to musculatures; cutis thin or absent ...... *Tubulanus floridanus*
3. Body light brown, without rings, but marked by numerous short, interrupted longitudinal lines of dark brown; lateral nerve cords internal to external longitudinal muscular layer; cutis thick ... *Baseodiscus delineatus*
4. Mouth small; body rounded in intestinal region; not adapted for swimming 5
4. Mouth large; lateral margins of body in intestinal region thin; adapted for swimming 7
5. Color red or rosy; body with slender caudal cirrus .... *Micrura leidyi*
5. Color brown or black; body without caudal cirrus 6
6. Color black, with pale anterior border of head .... *Lineus ater*
6. Color brown, with numerous paired transverse white markings on dorsal surface .... *Lineus stigmatus*
7. Color grayish blue or purplish with white anterior end; body slender throughout .... *Cerebratulus leucopsis*
7. Color grayish brown or rosy with numerous darker flecks on dorsal surface; body widest posteriorly .... *Cerebratulus fuscus*
8. Minute, slender, with single pair of conspicuous ocelli; parasites on crabs; stylet basis conical .... *Carcinonemertes carcinophila imminuta*
8. Broad and flat, with numerous ocelli; not parasitic; stylet basis crescentic *Drepanophorus crassus*

Order 1, PALEONEMERTEA

Family TUBULANIDAE

TUBULANUS FLORIDANUS Coe, 1951

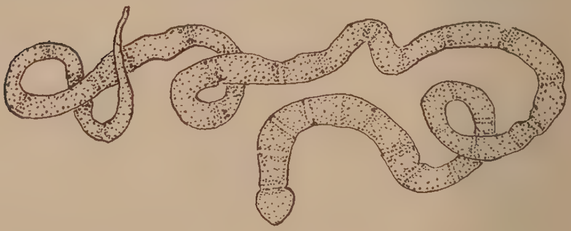

FIGURE 23. *Tubulanus floridanus*. Outline of body, showing narrow transverse whitish markings.

Body slender; the type specimen was 40 mm in length and only 1 to 2 mm in width after preservation. Head broad and flattened.

Color brown, with a series of very narrow rings, most of which completely encircle the body (Figure 23). In a worm 40 mm in length there were 30 rings. Anteriorly the rings are separated by a distance about equal to the diameter of the body but more posteriorly they are generally more widely separated and irregularly spaced.

The cerebral sense organs are large and the sensory cells are well demarcated from the adjacent spithelium. Median dorsal nerve larger than in most species of the genus.

At present known from only a single specimen collected on a dock piling in Biscayne Bay, Florida.

Individuals of this species have a superficial resemblance to those of *T. annulatus* (Montague), *T. capistratus* Coe and *T. nothus* Bürger but are without longitudinal lines of contrasting color.

Family BASEODISCIDAE

BASEODISCUS DELINEATUS (Delle Chiaje)

Polia delineata Della Chiaje, 1923-1929; *Baseodiscus delineatus* Diesing, 1850; *Eupolia delineata* Hubrecht, 1887; Bürger, 1890, 1895.

This species may be recognized in life by the extremely slender, but not fragile, body with broadly rounded head which is normally well demarcated from body (Figure 24). The length may sometimes exceed 500 mm but the width is seldom more than 2 mm except when the body is strongly contracted. A length of more than a meter has been reported.

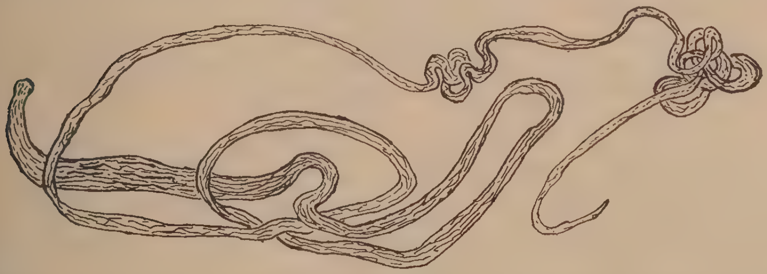

FIGURE 24. *Baseodiscus delineatus*. Outline showing extremely slender body and linear markings when fully extended. (After Bürger, 1895).

Color of body, including head, varies from light to dark brown, sometimes with greenish tinge, thickly covered with short, slender lines or interrupted longitudinal markings of darker shade both dorsally and ventrally (Figure 24, 25). Many variations of the color pattern have been reported. In addition to the typical form in which the lines are conspicuous, there are others in which the markings consist of indistinct and irregular rows of elongated dots.

Furthermore there is the broader and shorter form, *curtus,* considered by some to be a distinct species, in which the general coloration of the body varies from gray to deep red and the markings are indistinct. And finally there are individuals in which the ventral surface is colorless. In many widely separated localities the typical form and *curtus* are associated.

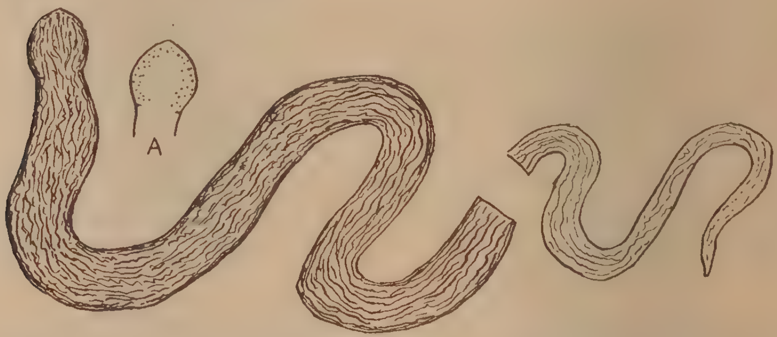

FIGURE 25. *Baseodiscus delineatus.* Outline of anterior and posterior ends of body, showing slender linear markings. *A*, head with numerous minute ocelli.

B. delineatus appears to be more widely distributed and in many places more abundant than any other species of nemertean, for it has been reported from the shores of nearly all the tropical and subtropical lands and islands where nemerteans have been collected. It occurs both in the northern and southern hemispheres, including the Mediterranean and Adriatic seas; Cape Verde Islands; Mauritius; Fifi Islands; Chile; Japan; Gulf of California; east coast of Africa; Java and other East Indian islands, Polynesia, Puerto Rico, Bermuda, Barbados, and the *curtis* form in Curaçao. On the Florida coast it has been found in Biscayne Bay.

Family LINEIDAE

LINEUS ATER (Girard)

Meckelia atra Girard, 1851; *Cerebratulus ater* Verrill, 1895; Stiasny-Wijnhoff, 1925; Coe, 1943.

This species was originally described from a single specimen dredged in deep water off the Cape of Florida. Two headless fragments which may have belonged to the same species were reported by Stiasny-Wijnhoff from Curaçao. The body is uniformly black in color except for the pale anterior extremity.

In the collections of the United States National Museum is a complete specimen 120 mm long and 4 to 6 mm wide. This was collected by Henry Hemphill on a reef at Key West, Florida, in January, 1885. In spite of its long preservation it still shows the characteristics of the species as described by Girard and obviously represents one of the relatively short and broad species of *Lineus*. The head and cephalic grooves are short but the mouth is rather large. The body is rounded in the intestinal region and does not have the thin lateral margins characteristic of *Cerebratulus*. Since the internal anatomy of this species is still unknown, it is regrettable that the state of preservation of this specimen makes it unsuitable for microscopical study.

LINEUS STIGMATUS Coe, 1951

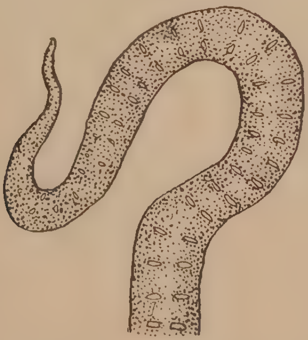

FIGURE 26. *Lineus stigmatus*. Diagram of posterior portion of body, showing arrangement of the paired white markings on dorsal surface.

Body rather slender, sometimes reaching a length of 150 mm or more and a width of 2 to 5 mm.

Color in life slaty brown on both dorsal and ventral surfaces, with paired transverse white markings on dorsal surface at intervals which average about half the width of the body (Figure 26). Each narrow marking is about one-fifth the width of the body in length and the two members of each pair are separated from the margin of the body and from each other by about the same distance. These markings become irregularly spaced and indistinct toward the posterior end of the body. The colors are retained after preservation for some weeks in alcohol.

Transverse sections of the body show an unusually thick cutis with many spiral muscular fibers and a heavily pigmented layer externally.

The color pattern in this species has a superficial resemblance to that of some individuals of *L. geniculatus* (D. Chiaje) in which the white rings are interrupted in the mid dorsal line but in the latter species the rings continue laterally and ventrally. There is also some resemblance to *L. albocinctus* Verrill, recorded from Bermuda and Puerto Rico, although in that species the transverse lines are continuous on the dorsal surface and the ventral surface of the body is whitish.

The species is at present known only from the shore of Biscayne Bay, Florida.

MICRURA LEIDYI (Verrill)

See preceding section.

CEREBRATULUS FUSCUS (McIntosh)

Micrura fusca McIntosh, 1873-4; *Cerebratulus fuscus* Bürger, 1892, 1895, 1904 (not *C. fuscus* Verrill, 1892).

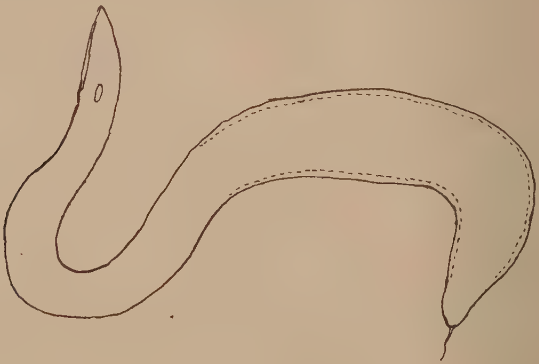

FIGURE 27. *Cerebratulus fuscus*. Outline of body, showing slender anterior portion and much wider posterior portion with caudal cirrus at end. The mouth and one of the cephalic grooves are indicated. Intestinal region with thin lateral margins adapted for swimming.

Differs from most other nemerteans in having the body slender anteriorly and much wider toward posterior end which is often sharply truncated in life but rounded when contracted. With slender caudal cirrus (Figure 27). Length of body 20 to 60 mm, width 2 to 6 mm. Head slender, not demarcated from body, with long cephalic grooves and large oval mouth.

Color grayish brown, flesh color or rosy, with pale lateral margins. Dorsal surface thickly speckled with more or less conspicuous dark flecks. Head with a yellowish or rosy hue.

Lives among algae, bryozoa and other growths in the lowest intertidal zone and below to depths of 100 meters or more. With a wide geographical distribution but most abundant on the coasts of England, Scotland, France and the Mediterranean. Reported also from South Africa. On the Florida coast this species has been found in Biscayne Bay.

In *C. luridus* Verrill, which occurs in deep water along the Atlantic coast from Nova Scotia to southern New England, the body is of similar shape but the two species differ widely in coloration and markings.

CEREBRATULUS LEUCOPSIS (Coe)

Micrura leucopsis Coe, 1902; Stiasny-Wijnhoff, 1925.

This species may be recognized by the grayish blue or purplish color of the body, with paler head and white anterior end. The body has smooth outlines, without corrugations when contracted; rounded in esophageal region and somewhat flattened posteriorly, with thin lateral margins. Length 50 to 100 mm. or more, width 3 to 6 mm.

Head narrower than body, roundly pointed anteriorly; cephalic grooves long and deep; mouth large. Caudal cirrus rather small; proboscis long and slender. No ocelli have been detected. The internal anatomy has been described by Coe (1902) and Stiasny-Wijnhoff (1925).

This appears to be a common and typical tropical species at depths of 20 meters or more. Four specimens were reported by Coe (1902) from Puerto Rico and seven by Stiasny-Wijnhoff (1925) from Curaçao. One specimen in the United States National Museum was collected by the U.S.F.C. Steamer ALBATROSS near Key West.

Order 3, HOPLONEMERTEA

Family CARCINONEMERTIDAE

CARCINONEMERTES CARCINOPHILA, var. IMMINUTA Humes, 1942

See section 1.

Family DREPANOPHORIDAE

DREPANOPHORUS CRASSUS (Quatr.)

Cerebratulus crassus Quatr., 1846; *D. crassus* Bürger, 1895; Coe, 1901; *Paradrepanophorus crassus* Stiasny-Wijnhoff, 1926.

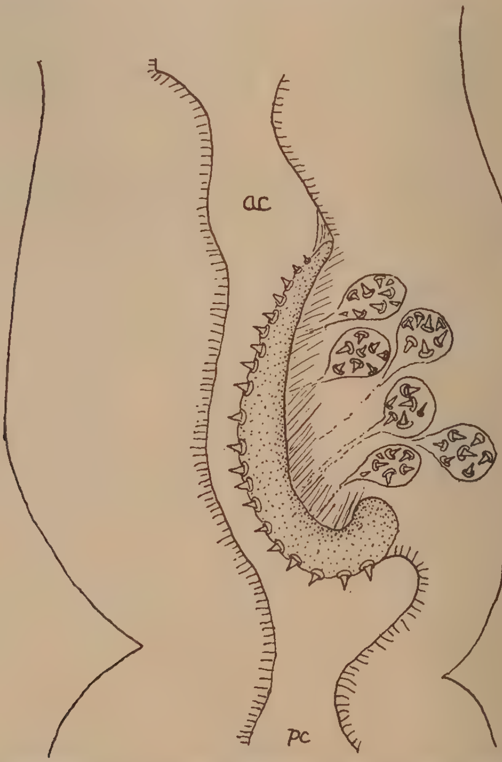

FIGURE 28. *Depanophorus crassus.* Diagram of armature of proboscis, showing sickle-shaped basis bearing 20 peg-like stylets and six of the pouches of accessory stylets. Anterior (*ac*) and posterior (*pc*) chambers of proboscis are indicated.

Body short, broad and much flattened; head narrow and usually well demarcated from body; mouth and rhynchodeal opening separate; proboscis sheath provided with lateral diverticula situated on dorsal side of intestinal diverticula, alternating with gonads; cerebral sense organs large, situated close beside and somewhat posterior to dorsal ganglia; lateral nerve cords lie on ventral side of body. Numerous large ocelli are arranged in two rows on each side of head.

Length of body when mature 20 to 50 mm, width 4 to 6 mm. Color of dorsal surface orange or yellow; ventral surface pale. Proboscis large, armed with sickle-shaped basis bearing about 20 peg-shaped stylets and a dozen or more pouches of accessory stylets (Figure 28). These are 19 or 20 proboscidial nerves.

This species has been reported from many tropical and subtropical seacoasts and elsewhere, including English Channel, Mediterranean Sea, Madeira, Samoa, Mauritius, Panama, Gulf of California, Peru and Puerto Rico but Stiasny-Wijnhoff (1926) has shown that some of these records actually pertain to other species. Found also near Key West, Florida.

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Made in United States of America

Reprinted from Journal of the Washington Academy of Sciences
Volume 41, No. 10, October 15, 1951

ZOOLOGY.—*Geographical distribution of the nemerteans of the northern coast of the Gulf of Mexico as compared with those of the southern coast of Florida, with descriptions of three new species.* Wesley R. Coe, Scripps Institution of Oceanography.[1] (Communicated by W. L. Schmitt.)

Up to the present time no published information has been available relative to the nemerteans of the areas covered by this report. Consequently it has been uncertain whether the nemertean fauna might be found to consist principally or wholly of species identical with those of the Atlantic coast or whether the more typically tropical or subtropical species would be included. Nor was it known whether any or many apparently endemic forms might be present.

Twenty-two species have now been identified. Sixteen of these are found on the northern coasts of the Gulf and six others in southern Florida. Only two specimens from the deeper, off-shore waters of the Gulf have been obtained by the writer. Both of these belong to either *Lineus* or *Micrura*, but the specimens were not sufficiently well preserved to allow specific analysis. No information is yet available for all that portion of the western Gulf coast south of the Mexican border, or for any locality on the west coast of the Florida peninsula between Franklin County and Key West.

The presumable explanation for the small number of species at present known is that only sporadic efforts have been made toward a complete survey of the littoral fauna of the Gulf. On the Atlantic coast of North America there are 53 known species of nemerteans and on the Pacific coast 95 species. Hence it seems probable that there are many more species now actually living in the Gulf than can be included in this report.

Even on the Atlantic coast the nemerteans have been studied extensively only as far south as New Jersey, and our knowledge of the species living between that State and Florida is based on collections made at widely separated localities. It may therefore be assumed that some, perhaps many, additional species remain to be discovered there.

All except two of the species known from the northern part of the Gulf are also found on the Atlantic coast. Therefore, it seems probable that the nemertean fauna of the northern Gulf coast has in the past been a continuation of that of the Atlantic coast and that it is now a separate fauna that was isolated in Pleistocene times by the Florida Peninsula. To determine whether any of the populations of the two areas are at present continuous, it is essential to obtain additional collections on both sides of the southern half of that peninsula. It is already known that the species found at Pensacola, on the Gulf side, are similar to those found by the writer personally at St. Augustine, on the Atlantic side. The following lists, however, indicate that these two nemertean faunas are separated by an area in which other species predominate.

Because the nemerteans of the northern Gulf coast are generally of different species than those at present known from southern Florida, the species of the two areas will be listed separately.

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[1] Contribution from the Scripps Institution of Oceanography, new series, no. 539.

I. GEOGRAPHICAL DISTRIBUTION OF SPECIES AT PRESENT KNOWN FROM THE NORTHERN COAST OF THE GULF OF MEXICO

[Abbreviations indicate: A, Atlantic coast of North America; E; coasts of Europe; G, Northern coast of the Gulf of Mexico; P, Pacific coast of North America; S, southern Florida; W, West Indies; X, at other localities.]

Order 1, PALEONEMERTEA

Family Tubulanidae

Tubulanus pellucidus (Coe), 1895. A, G, P.

Family Carinomidae

Carinoma tremaphoros Thompson, 1900. A, G.

Order 2, HETERONEMERTEA

Family Lineidae

Zygeupolia rubens (Coe), 1895. A, G, P.
Lineus socialis (Leidy), 1855. A, G.
Micrura leidyi (Verrill), 1892. A. G. S.
Cerebratulus lacteus (Leidy), 1851. A, G.

Order 3, HOPLONEMERTEA

Family Emplectonemertidae

Paranemertes biocellata Coe, 1944. G.

Family Carcinonemertidae

Carcinonemertes carcinophila (Kölliker), 1845. A, E. G.
Carcinonemertes carcinophila imminuta Humes, 1942. G, S, W.

Family Prosorhochmidae

Oerstedia dorsalis (Abild.), 1806. A, E, G, P, X.

Family Amphiporidae

Zygonemertes virescens (Verrill), 1879. A, G, P.
Amphiporus cruentatus Verrill, 1879. A, G, P.
Amphiporus ochraceus (Verrill), 1873. A, G.

Amphiporus texanus, n. sp.

This new species represents one of the larger and broader forms of this extensive genus. The type specimen was about 60 mm in length and 6 mm in width after preservation. The length of this specimen is therefore only 10 times the greatest width. The head is narrow, about 2 mm in width, with subterminal mouth and transverse or oblique lateral grooves. There are many small ocelli on each side of the head, although the exact number and arrangement could not be determined in this specimen.

The proboscis is large and extends nearly the entire length of the body. The central stylet is moderately slender and about two-thirds of the length of the relatively massive basis. The latter is nearly rectangular in outline, about four times as long as its diameter, tapering but slightly toward the anterior end and is truncated posteriorly (Fig. 1). In this type specimen the basis measured 0.135 mm in length and from 0.027 to 0.035 in diameter. One of the two accessory pouches contained two well-formed stylets and the other had three, two of which were not yet completed. In this specimen there were 10 rather large proboscidial nerves.

No record is available regarding the color in life, but the specimen preserved in formalin indicated a pale, reddish-brown epidermal pigmentation. The cerebral sense organs are comparatively larger than in most species of the genus. They are situated lateroventrally and a short distance anterior to the brain.

This specimen (U.S.N.M. no. 22965) was collected by B. Earp at Port Aransas, Tex. All the other species of nemerteans at present known from that locality are found also on the North Atlantic coast. Consequently it is uncertain whether this new species is limited to the Gulf of Mexico or whether it may occur also on the Atlantic coast, although it has not yet been found there.

Family Tetrastemmatidae

Tetrastemma candidum (Müller), 1774. A, E, G, P. X.
Tetrastemma vermiculus (Quatr.), 1846. A, E, G.

Order 4, BDELLONEMERTEA

Family Malacobdellidae

Malacobdella grossa (O. F. Müller), 1776. A, E, G, P.

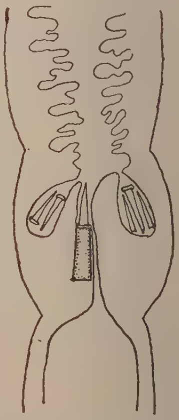

FIG. 1.—*Amphiporus texanus* n. sp.: Outline of stylet apparatus of proboscis.

II. SPECIES AT PRESENT KNOWN FROM SOUTHERN FLORIDA

Order 1, PALEONEMERTEA

Tubulanus floridanus, n. sp.

In the collections from Biscayne Bay, Fla., was one specimen of *Tubulanus* that evidently represents a previously undescribed species. This specimen is very slender, about 40 mm in length and only 1 to 2 mm wide. The color in life is brown, with a series of about 30 very narrow rings of lighter color. Nearly all the rings completely encircle the body. Anteriorly the rings are separated by a distance about equal to the diameter of the body but more posteriorly they are generally more widely separated and irregularly spaced. The lateral sense organs can be distinguished externally but are not conspicuous.

Transverse sections show a rather thick outer epithelium, with a thin, but dense, basement layer and an unusually large median dorsal nerve. The cerebral sense organs are large and highly specialized, with a sensory canal leading laterally to the surface of the epithelium.

Individuals of this species have a superficial resemblance to those of *T. annulatus* (Montague), *T. capistratus* Coe, and *T. nothus* (Bürger) but are without longitudinal lines of contrasting color.

One individual of this species was collected by F. M. Bayer among algae on dock piling on the County Causeway at Miami, Biscayne Bay, Florida. U. S. Nat. Mus. Cat. No. 22251.

Order 2, HETERONEMERTEA

Family Lineidae

Lineus ater (Girard), 1851. S, W.

Lineus stigmatus n. sp.

The collections contained fragments of an undescribed species of this genus, but unfortunately the head was not among them. Nevertheless the markings on the body are so distinctive as to indicate that these fragments could not have belonged to any of the numerous described species. It seems necessary therefore to give as complete a diagnosis of a new species as is possible in the absence of the head.

The fragments have a maximum width of 5 mm, tapering to about 2 mm at the posterior end, indicating that the entire individual would have had a length of 150 mm or more.

The color in life was slaty brown on both dorsal and ventral surfaces, with paired transverse white markings at intervals of 1 to 2 mm on the dorsal surface. Each narrow marking is about one-fifth the diameter of the body in length and the two members of each pair are separated from the margin and from each other by about the same distance (Fig. 2). The markings are limited to the dorsal surface and become irregular and indistinct toward the posterior end of the body. The colors are retained after preservation in alcohol.

Since the anterior end of the body was not obtained, nothing can now be said as to the presence of ocelli, the character of the cephalic grooves or other sense organs or the peculiarities of the nephridia. Transverse sections of the body show an unusually thick cutis with many spiral muscular fibers and a heavily pigmented layer externally.

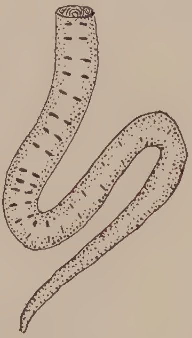

FIG. 2.—*Lineus stigmatus* n. sp.: Outline of posterior portion of body, showing position of white markings. The markings appear to be irregularly spaced, owing to differences in state of contraction.

The paired markings in this species have a superficial resemblance to those of some individuals of *L. geniculatus* (D. Chiaje) in which the white rings are interrupted in the mid dorsal line but in the latter species the rings continue laterally and ventrally. There is also some resemblance to *L. albocinctus* Verrill, recorded from Bermuda and Puerto Rico, although in that species the transverse lines are continuous on the dorsal surface and the ventral surface of the body is whitish.

The species is at present known only from the fragments of one individual collected by G. S. Posner on the shore of Biscayne Bay, Fla. U.S.N.M. no. 22252.

Micrura leidyi (Verrill), 1892. A, G, S.
Cerebratulus fuscus McIntosh, 1873. E, S, X.
Cerebratulus leucopsis (Coe), 1902. S, W.

Order 3, Hoplonemertea

Family Amphiporidae

Carcinonemertes carcinophila var. *imminuta* Humes, 1942. G, S, W.

Family Drepanophoridae

Drepanophorus crassus (Quatr.), 1846. E, P, S, W, X.

SUMMARY

The preceding lists show that many of the species have a remarkably wide geographical distribution already recorded and it may be expected that they will later be found elsewhere. Of the 16 species at present known from the northern Gulf coast, all except *Paranemertes biocellata* and *Amphiporus texanus* are widely distributed on the American Atlantic coast, and four of them, namely, *Tubulanus pellucidus*, *Zygeupolia rubens*, *Zygonemertes virescens*, and *Amphiporus cruentatus*, occur also on the Pacific coast but not in Europe; two others, *Carcinonemertes carcinophila* and *Tetrastemma vermiculus*, are found on American Atlantic and European coasts but not in the Pacific; *Oerstedia dorsalis* and *Tetrastemma candidum* are circumpolar, being distributed along both the east and west Atlantic and Pacific coasts; *Malacobdella grossa* occurs on both American coasts and in Europe; while the remaining five species, *Carinoma tremaphoros*, *Lineus socialis*, *Micrura leidyi*, *Cerebratulus lacteus*, and *Amphiporus ochraceus* are known only from the Atlantic and Gulf coasts. *Paranemertes biocellata* and *Cerebratulus texanus* have been found only on the northern Gulf coast and may possibly represent endemic species.

Of the seven species herein recorded from southern Florida, only two are known to occur both on the northern Gulf coast and in southern Florida, while *Lineus ater* and *Cerebratulus leucopsis* have been previously reported from Puerto Rico and Curaçao. *Cerebratulus fuscus* occurs also in northern Europe and South Africa, while *Drepanophorus crassus* has an almost world-wide distribution. *Tubulanus floridanus* and *Lineus stigmatus* are at present known only from Biscayne Bay, Fla.

For comparison, it may be noted that 11 of the 53 species found on the North American Atlantic coast are identical with species in European waters, while 12 of the Atlantic coast species occur also on the Pacific coast and 2 of these extend also to Japan. No less than 18 of the species found on the Pacific coast are thought to be identical with well-known European species and others are closely similar.

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Reprinted from JOURNAL OF MAMMALOGY
Vol. 32, No. 4, November, 1951, pp. 403–410
Printed in U.S.A

EASTERN PACIFIC RECORDS AND GENERAL DISTRIBUTION OF THE PYGMY SPERM WHALE

By CARL L. HUBBS

Though now regarded by cetologists as a cosmopolitan species less rare than it was previously thought to be, the pygmy sperm whale, *Kogia breviceps* (Blainville), has been reported only three or four times from the vast length of the eastern Pacific shoreline. Until very recently, in fact, the only New-World Pacific record was that of "Lower California," from which assigned type-locality Gill (1871, p. 736) described the nominal species, *Kogia floweri*, with the hope, long unfilfilled, "that this article may incite our California friends to seek for and procure specimens." This indefinite and inclusive locality was presumably incorrect, for Lyon and Osgood (1909, p. 4) stated that the type material (No. 8016, United States National Museum), comprising a mandible and a water-color sketch, was from "off Mazatlan, Sinaloa, Mexico." Hirasaka (1937, p. 120), presumably on advice from Glover M. Allen, listed the locality as "off Mazatlan, Lower California" and Allen himself (1941, pp. 19 and 23) gave it both as "near Mazatlan, Mexico" and as "Lower California." Trusting the museum record, we assume that the specimen was taken in the vicinity of Mazatlán, Sinaloa, México, near the mouth of the Gulf of California, in warm water with a definitely tropical fauna.

The second eastern Pacific record was added by Hirasaka (1937, p. 122), on word from Glover M. Allen, as "Independentia, Peru." Allen (1941, p. 19) repeated the record, as "beach at Independencia Bay, Peru," adding that the specimen was "interesting as occurring in the region of the cool Humboldt Current, though it may, of course, have washed in from a warmer area of the adjacent seas." Its provenance from warm water seems highly improbable and, in view of the next record, quite unnecessary to assume.

A third record from the eastern Pacific (the second from the northeastern Pacific) has just been given by Scheffer and Slipp (1948, pp. 307–309, figs. 41–42) on the basis of a young male specimen that was washed ashore on the cold outer coast of Washington. They add an additional plausible though hearsay record from near Cape Flattery, Washington.

First California record.—The first California record is based on one of the photographs (Pl. I), now deposited in the Scripps Institution of Oceanography, that were collected by the well-known marine game-fish sportsman and author, Charles Frederick Holder. On its reverse side the print carries the notation "Sept. 6, 1936/opp. end of 25th St. on Beach/Balboa, Calif." Since Holder was a competent naturalist, there can be very little doubt as to the authenticity of the data.

It is obvious that this photograph represents an adult pygmy sperm whale. It corresponds very well with the photographs published by Scheffer and Slipp and almost surely represents the same species, whether or not more than one kind of *Kogia* be recognized. Agreement is good in the dark color; in the short flippers; in the laterally turgid head, with the eyes at the summits of bulbous swellings (presumably exaggerated by the shrinkage of the snout); in the very strongly projecting and bluntly pointed snout; and in the short, inferior, anteriorly rounded mouth, with the sides of the gape rather strongly divergent posteriorly. It certainly does not represent a young sperm whale, *Physeter catodon* Linnaeus, for the head and the jaws are of quite different shape. It resembles no recognized species other than *Kogia breviceps*. Dr. Remington Kellogg has concurred in this identification.

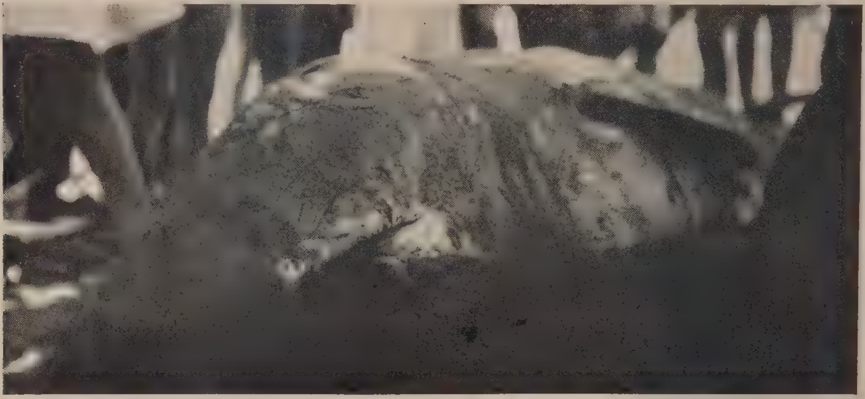

PLATE I

Specimen of pygmy sperm whale stranded at Balboa, on September 6, 1936. From photograph in collection of Charles Frederick Holder

Second California specimen.—The second specimen came ashore during a violent onshore storm, presumably on the night of December 9, 1949. Still alive, it was discovered by Ray Riggin of Imperial Beach about 8:00 A.M. on December 10, on the sand beach opposite Tijuana Slough about one-fourth mile north of its outlet, between San Diego Bay and the Mexican border. Mr. Riggin promptly notified Scripps Institution of the find. Following our advice he, with the help of neighbors, tethered the odd beast by a hauser to a steel stake, to prevent it being washed to sea by the incoming tide. The *Kogia* was still breathing when I arrived on the scene about 10:30 A.M., with volunteer assistants from the Institution. After washing down the somewhat desiccated skin with water from the surf, we rolled the little whale onto a tarpaulin and dragged it across the sandspit into the lagoon. We then pulled it by the heavy rope, tail first, toward the end of the road about one-half mile north. Gradually, in its natural medium, the animal recovered enough strength to give several of us quite a struggle. About noon we pulled it over a timber ramp onto a stake truck, covered it with wet blankets and then hastily drove to Scripps Institution. On arrival about an hour later the whale gave proof of having survived the trip by breathing heavily, but

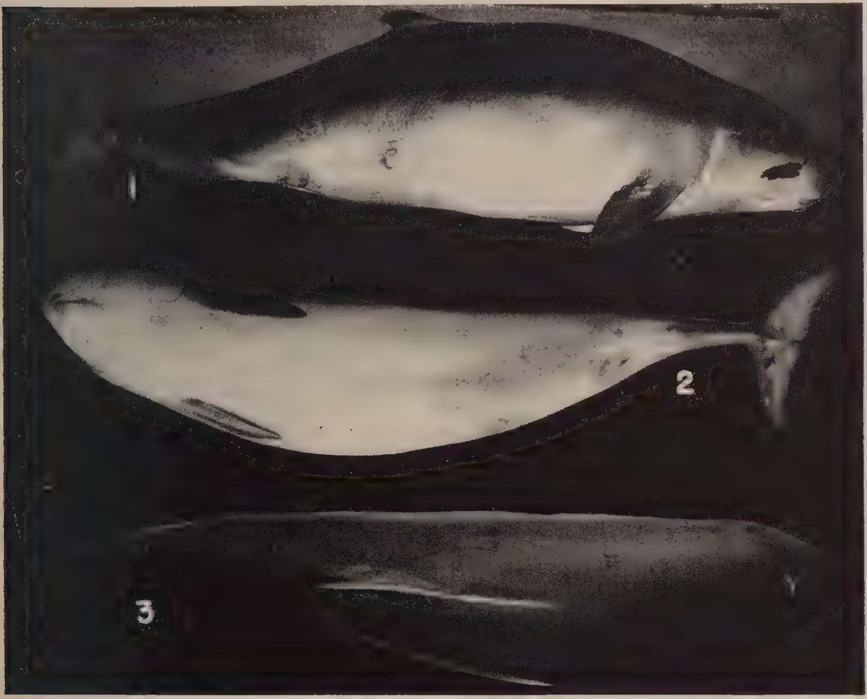

PLATE II

Lateral, ventral, and dorsal views, respectively, of a pygmy sperm whale collected near Imperial Beach, December 10, 1949. Photographs by John B. MacFall, Scripps Institution of Oceanography, December 11, 1949

it failed to recover despite efforts at artificial respiration, after being promptly immersed in an adequately large concrete tank.

During the following day the choice specimen, still in excellent condition, was photographed from various angles (Pls. II–III), measured thoroughly (Table 1), cast by Leon J. Pray for a lifelike display now on exhibit at the San Diego Museum of Natural History, and completely skeletonized for the growing cetacean collection of the San Diego Society of Natural History. Samples of the blubber were utilized in underwater sound research at Scripps Institution. Neither time nor energy was left for any extensive dissection or description of

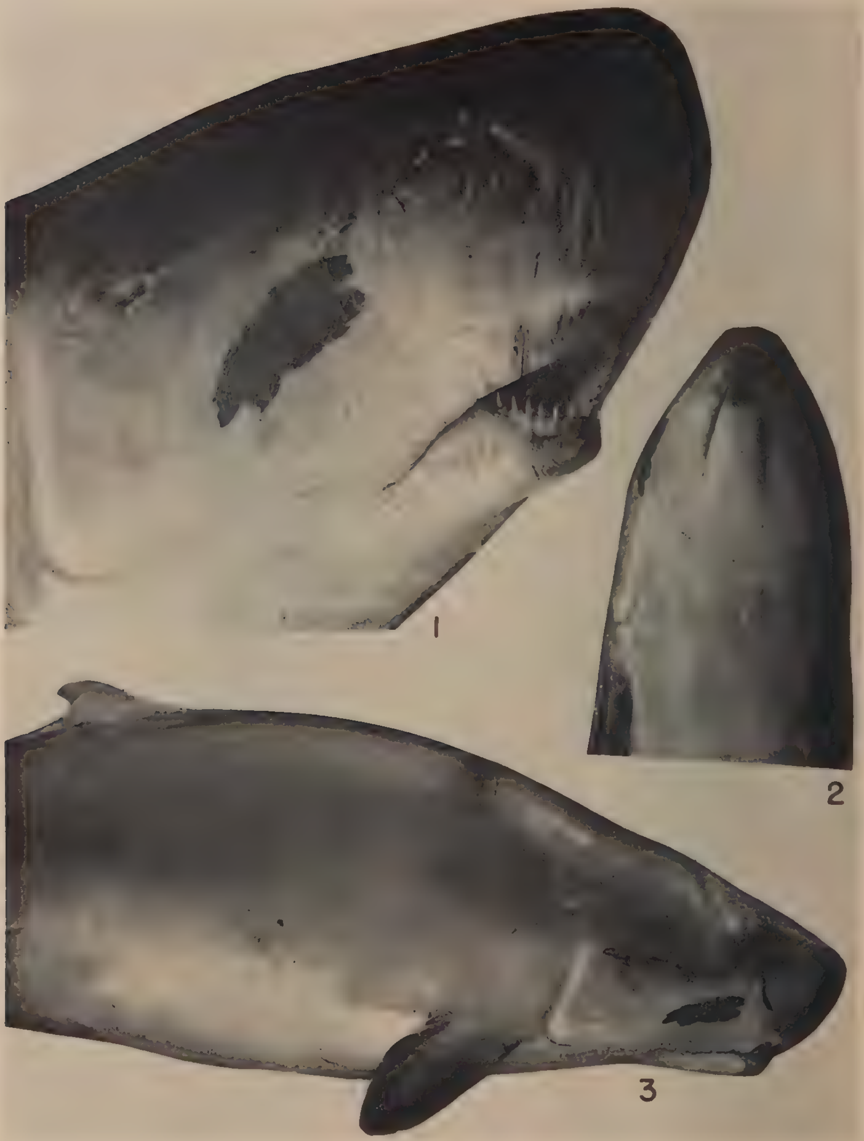

PLATE III

Pygmy sperm whale collected near Imperial Beach, California
(1) Oblique view of mouth, showing teeth
(2) Ventral view of head, showing form, mouth, and coloration
(3) Detail of anterior lateral parts, showing texture, coloration, and parasitic copepod

TABLE 1.—*External measurements of pygmy sperm whale from near Imperial Beach, California*

All measurements, except circumference, were made in a straight line between specified points

Total length (mm.) from tip of snout to: Farthest tip of flukes	2490
Line joining tips of flukes	2465
Notch at middle of flukes	2345
Proportions in thousandths of length to notch in flukes	
Greatest half-circumference (on one side of body)	330
Distance from tip of snout to line of greatest circumference	394
Depth of body: From origin of dorsal fin to end of genital slit	246
Over front of anal slit	178
At origin of flukes	70
Width of body: Greatest width	190
Least width	26
Opposite front of mouth	74
From eye to eye	157
Opposite middle of anus	88
Least distance between flippers	96
From tip of snout to: Front of mouth	82
Front of blowhole	116
Front of eye	156
Insertion of flipper	246
Tip of flipper	379
Front of dorsal fin	499
Tip of dorsal lobe	638
Front of genital slit	429
Front of anal slit	685
Length of external genital slit	75
From rear of genital slit to front of anal slit	217
Length of anal slit	43
From rear of anal slit to notch in flukes	281
Gape from inside of upper lip: To internal end of gape	44
To extreme end of crease	70
Between ends of crease of gape	37
From end of gape to insertion of flipper	128
Blowhole width	30
Orbit length	9
From orbit to: Blowhole	94
Corner of gape	83
Insertion of flipper	105
Flipper: Insertion to tip	134
Basal width	66
Greatest width, near middle	54
Dorsal fin: Origin to tip	147
Vertical height	66
Flukes: Greatest overall width	242
From notch to tip	132
From origin to notch	87

the internal anatomy. The external characteristics, however, were noted in some detail.

Description of the Imperial Beach specimen.—In top view (Pl. II, 3) this unbloated specimen was slick and streamlined, with a rather sharply pointed snout and a very slender caudal peduncle. The area of greatest cross-section was located at 37 per cent of the distance from the entering wedge to the end of the tail race—approximately at the location (36 per cent) to be expected in a perfectly streamlined body. In side view (Pl. II, 1 and Pl. III, 3) the head was subrectangular, with a steep curve from the preposterously small mouth to the very broadly rounded snout. The dorsal contour was slightly convex in a region just above and behind the eyes and was gently curved between the nape and the dorsal fin. As seen from below (Pl. III, 2), the head was very broad behind the subconical snout, with only a slight bulge in the general region of the eyes. The high dorsal keel of the caudal peduncle was weakly continued forward into the postdorsal keel (Pl. II, 3). The form of the fins is shown in the figures.

The upper parts were dark gray with a somewhat bluish tinge, becoming almost black dorsally. The head was dark downward well toward the mouth and in a circle around the eye. About halfway between the eye and the tip of the snout the light color extended upward to well above the middle of the height of the head. The tip of the chin and the adjacent parts of the snout were dark (Pl. III). There was a large jet-black blotch on the right side, between eye and mouth. The dark color of the back, diluted to gray, extended downward to the blackish-topped flippers and to the same level for some distance backward (Pls. II and III). Behind this area, the whitish to light-gray ventral color extended across the lower half of the trunk. Behind the anus the dark color dropped downward to cover the ventral keel and, with some dilution, the lower surface of the flukes. The flippers became abruptly white on the inner surface (Pl. II).

A pair of very striking bracket-like marks, which I have not seen figured or described, were symmetrically disposed on the two sides of the head between the eye and the flippers (Pl. II, 1; Pl. III). Most of the mark, including all of the upper part, was whitish, but the lower parts were bounded behind by a blackish streak that became narrower and darker around the lower hook. This mark looked strangely like the gill opening of a teleost fish, but I see no significance in this resemblance.

At the forward-hooked upper end of this mark, not far behind the eye, there was the small external opening of the ear (Pl. III). Charles L. Camp informs me that he found the ear opening at this end of the color mark in an adult female, that was stranded years ago near New York, and in its embryo, and, further, that he located, in both the female and the embryo, near the lower end of the mark, an opening that led into a large, presumably glandular, cavity. It seems probable that the mark is characteristic of the genus.

The few slightly incurved needle-like teeth diverged rather strongly on the sides of the mandible (Pl. III, 1).

No pathological conditions were noted to which the stranding or death of the creature could be ascribed. A very large copepod of the genus *Pennella* (Pl. III, 3) was attached dorsolaterally, about equidistant from eye and snout tip. On the right flank in advance of the anus there was a large curved scar, well healed (Pl. II, 1). There were other healed scars, possibly produced by other males in combat, on the side of the snout (Pl. III). The stomach was empty.

Sex and maturity.—Despite its small size, less than 8 feet overall, the Imperial Beach specimen was an apparently mature or nearly mature male. The scars just mentioned suggest maturity. The skull bones seemed to be thoroughly ankylosed. Each testis was about 1 x 4 inches in size and the penis was about 18 inches long.

It may be a coincidence, of course, that the specimen reported from Washington by Scheffer and Slipp was also a male, but it may well be that only males wander far to the north. That is the habit of the sperm whale, *Physeter catodon* Linnaeus. Confirming published accounts, officials of the two whaling stations that have been operating recently off western North America (at Fields Landing, northern California, and at Coal Harbour, British Columbia) have reported that they have very seldom taken a female sperm whale.

Distributional considerations.—Geographically and ecologically, these record stations in southern California nicely bridge the broad gap between the previously reported regions of occurrence on the Pacific Coast of North America, namely in the Gulf of California and in Washington.

No critical consideration is here given to the current view that all kogiids are referable to a single species. The accepted idea of the cosmopolitan distribution of a single species finds support in the broad distribution of pygmy sperm whales through tropical and temperature seas, as determined and mapped by Hirasaka (1937, pp. 119–122, map 1) and as confirmed by the more recent reports, including Edmondson's (1948) records from the Hawaiian Islands.

The new eastern Pacific records, however, do not confirm Hirasaka's opinion that in temperate regions *Kogia* is confined to warm currents of tropical origin and that the young are found only in the more tropical parts of the range. The three or four recent Pacific records all lie in regions of cool currents and much upwelling, far from flows of tropical origin. Similarly, the east coast of the South Island of New Zealand and the southwestern tip of Africa, from each of which there are several records, are not subtropical. The relatively numerous records from the east coast of North America, from Florida to Nova Scotia (Allen, 1937, pp. 19–24), do suggest an especial abundance in waters tempered by the Gulf Stream, but the few reports from Japan (Hirasaka, 1937) hardly justify the generalization that the pygmy sperm whales are commonest in warm currents of tropical origin. Nor does the small size (1885 mm. to notch in flukes) of the specimen from near Grayland, Washington, confirm Hirasaka's opinion that the young occur only in the more tropical parts of the range of the species. We may conclude that *Kogia* is widely distributed around the world in temperate as well as tropical waters.

Kogia breviceps is the third recent addition to the known whale fauna of the western United States. The other two are the beaked whales, *Mesoplodon bowdoini* Andrews and *Ziphius cavirostris* Cuvier (Hubbs, 1946, and subsequent reports for *Ziphius*).

Gastronomic considerations.—Having enjoyed eating the flesh of the *Mesoplodon* reported in 1946 (it was particularly welcome during the war-time period of red-meat shortage), the staff of Scripps Institution and friends ate a large part of the deep-red flesh of the pygmy sperm whale. Reports ranged from disgust to enthusiasm. I thought this flesh to be somewhat stronger in flavor and less delectable than that of the beaked whale. No ill effects were experienced by any who partook of the meat of either species. In this connection we may recall published statements to the effect that the flesh of beaked whales is considered poisonous in Norway (a supposition that may well be unfounded) and that sperm whales (*Physeter*) are rated low as human food.

Acknowledgments.—I am happy to express appreciation to Ray Riggin of Imperial Beach, who found the pygmy sperm whale just discussed, secured it, and aided in its transport, and to various colleagues and students at Scripps Institution, including Sam D. Hinton, W. E. Barraclough, Al. A. Allanson, Frederick H. C. Taylor, and, as usual, my good wife, Laura. Remington Kellogg, Victor B. Scheffer, and Charles L. Camp generously furnished data.

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Scripps Institution of Oceanography, University of California, La Jolla, California. *Received February 3, 1951.*

[Contributions, New Series, No. 540]

AN AUTOMATIC REAGENT DISPENSER FOR SHIPBOARD USE[1]

BY

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Scripps Institution of Oceanography, La Jolla, California

Recent work on modification of the molybdenum-blue method for determination of dissolved inorganic phosphate in sea water (Wooster and Rakestraw, 1951)[3] showed the need for a simple rugged device suitable for rapid and precise delivery of small quantities of reagents at sea. The two reagents used for phosphate determination impose additional requirements on this device. Molybdic acid solution must be protected from the light and must not be allowed to come in contact with rubber; stannous chloride solution must be protected from contact with the atmosphere.

An automatic reagent dispenser which meets these requirements is shown in Figs. 1 and 2. Volume of reagent delivery is governed by travel of the spring-loaded syringe plunger, which in turn is controlled by a series of carefully machined steps. Dimensions of these steps are determined by bore of the syringe plunger and by delivery volume required. The syringe assembly, acting through a length of Tygon tubing, pumps mineral oil which comes in contact with the reagent solution at an oil-reagent interface. After the delivery system of the dispenser has been loaded by withdrawal of the plunger, unit delivery of reagents is effected by stepwise release of the plunger. In order to protect reagents from light and glassware from breakage, glassware and reagent bottle are customarily enclosed in a wooden box. This box is provided with an opening into which can be inserted the sample bottle to which reagents are to be added.

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[1] Contributions from Scripps Institution of Oceanography, New Series, No. 541. This work was supported by the Marine Research Committee, Department of Natural Resources, State of California.

[2] Present address: Johns Hopkins University, Baltimore, Maryland.

[3] Wooster, W. S. and N. W. Rakestraw, The estimation of dissolved phosphate in sea water, J. Mar. Res., *10* (1): 91–100, 1951.

Reprint from SEARS FOUND. JOURN. MAR RES.

Two such dispensers were calibrated by weighing deliveries of distilled water. One dispenser made 20 deliveries, using each step in succession, with an average volume of 0.205 ml and a standard deviation of 0.004 ml; the other dispenser made 20 deliveries with an average volume of 1.002 ml and a standard deviation of 0.010 ml.

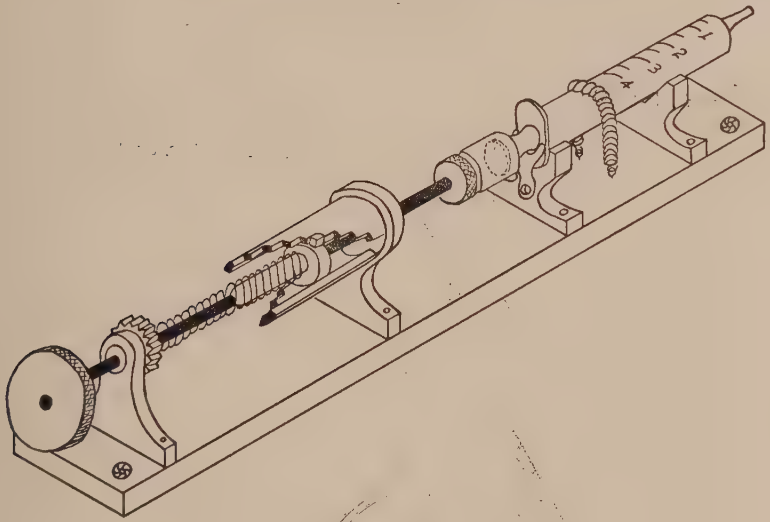

Figure 1. Syringe assembly for delivery of 0.50 ml.

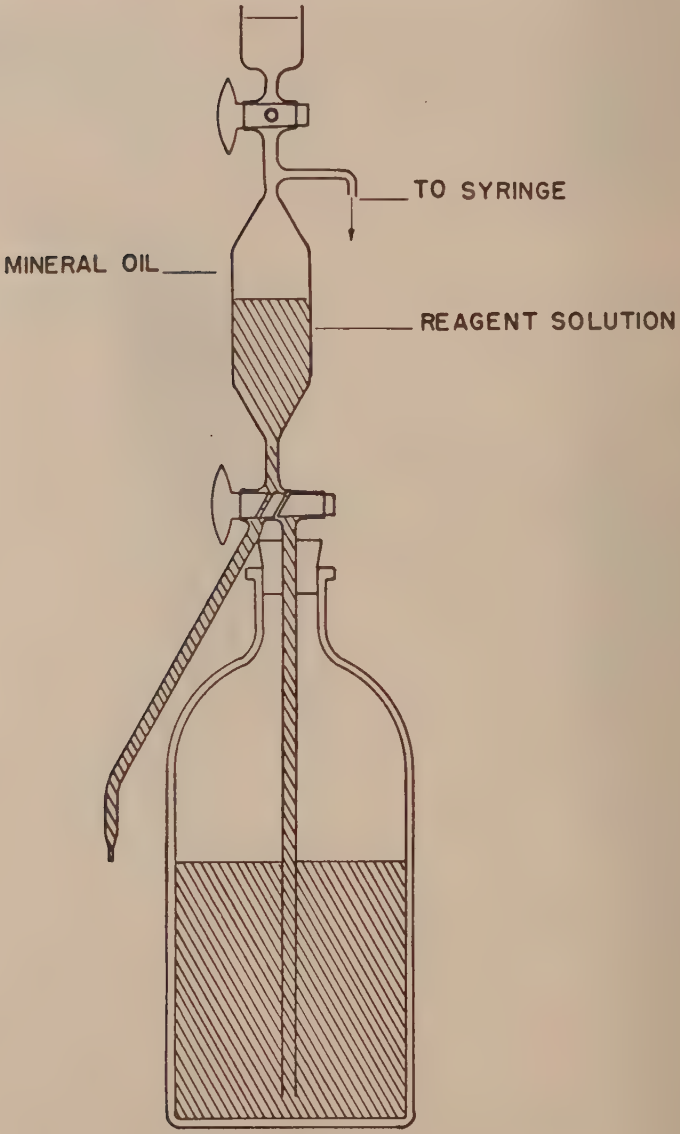
TO SYRINGE
MINERAL OIL
REAGENT SOLUTION

Figure 2. Glassware for automatic reagent dispenser.

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NUMBER 535 DECEMBER 11, 1951

OCCASIONAL PAPERS OF THE MUSEUM OF ZOOLOGY

UNIVERSITY OF MICHIGAN

ANN ARBOR, MICHIGAN UNIVERSITY OF MICHIGAN PRESS

STATUS, SUBSPECIES, AND VARIATIONS OF *NOTROPIS CUMMINGSAE,* A CYPRINID FISH OF THE SOUTHEASTERN UNITED STATES*

BY CARL L. HUBBS AND EDWARD C. RANEY

INTRODUCTION AND ACKNOWLEDGMENTS

FOR many years it has been evident that the southeastern states of the United States constitute one of the most fertile fields for ichthyological discoveries. In each of the stream systems of that region the student of fishes may find new kinds, or new facts regarding the status, distribution, and life ways of forms already described. This is particularly true of the smaller fishes, including the almost endless array of shiners comprising the genus *Notropis.* In addition to the present paper dealing with the dusky shiner, *Notropis cummingsae* Myers, 3 reports on the southeastern species of *Notropis* have been prepared recently (Hubbs, 1941; Hubbs and Raney, 1947, 1948).

We wish to acknowledge especially the assistance of Reeve M. Bailey, curator of fishes, Museum of Zoology, University of Michigan, who made available the specimens under his care, some of which he and Marian K. Bailey had collected. He also provided certain fin ray counts and performed other services. Specimens of critical value were kindly furnished by Leonard P. Schultz, curator of fishes, United States National Museum, E. Milton Burton of the Charleston Museum, F. E. Guyton of the University of Alabama, Elmer E. Brown of Davidson College, Harry W. Freeman of the University of South Carolina (now at Stanford University), and Donald J. Ameel, now of Kansas State College. Other collections were made by Edwin P. Creaser and Herbert R. Becker, O. K. Fletcher, Jr. and W. H. Fletcher, William

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* Contributions from the Scripps Institution of Oceanography, New Series, No. 542, from the Museum of Zoology of the University of Michigan, and from the Department of Conservation of Cornell University

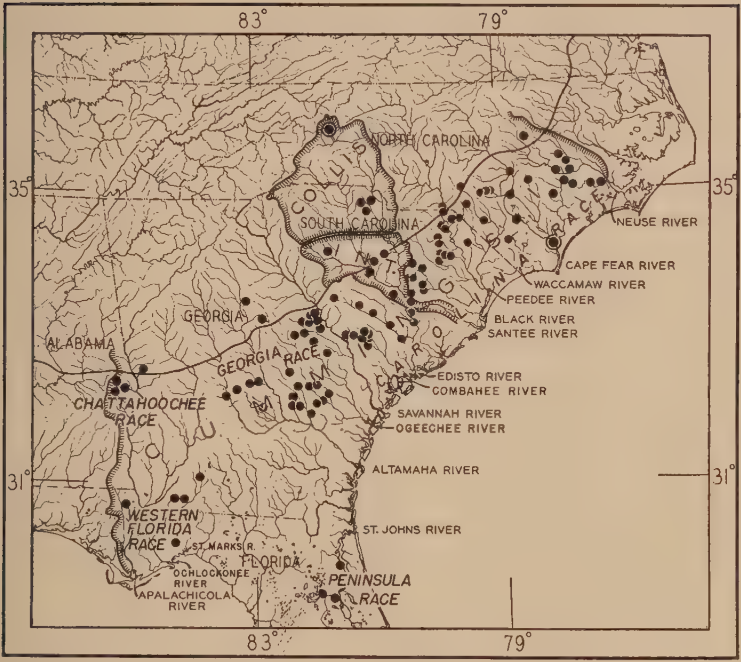
M. McLane and Gil Nelson, O. C. Van Hyning, and C. R. Aschemeir. To all of these collectors we express our gratitude. For aid in processing data we again owe thanks to Laura C. Hubbs.

The field work of the junior author was supported by grants from the Trustee–Faculty Research Committee, Cornell University. He was ably assisted at various times in the field by the following graduate students from Cornell: Richard H. Backus, Howard E. Evans, Warren J. Houck, L. James Kezer, Ernest A. Lachner, Roman A. Pfeiffer, C. Richard Robins, Robert M. Roecker, Robert D. Ross, and Royal D. Suttkus. Suttkus has further assisted by adding much material from new regions on three collecting trips which he led. During the summer of 1948 he was assisted by Merlin Suttkus; in June, 1949, by Charles F. Cole and Robert H. Gibbs, Jr.; and in December, 1949, and January, 1950, by Charles F. Cole, Roland L. Wigley, and Ralph W. Yerger. Edward E. Hueske made collections in the summer of 1946.

GENERAL DISTRIBUTION

In its various local forms *Notropis cummingsae* ranges from the Neuse River system in east-central North Carolina through the Cape Fear, Waccamaw, Peedee, Black, Santee, Edisto, Combahee, Savannah, Ogeechee, and Altamaha drainage basins of the Carolinas and eastern Georgia to the St. Johns River system in northeastern Florida and to the St. Marks, Ochlockonee, and Apalachicola River systems in western Florida, southwestern Georgia, and southeastern Alabama (Map 1). Like some other species it seems to avoid most of the Florida peninsula. Except in the Santee River system, where its upland subspecies, *N. c. collis,* ranges across the Piedmont into the Mountains, it is essentially a fish of the Coastal Plain (including the relatively low Tifton Upland), only rarely, locally, and to a limited distance passing above the Fall Line (Map 1). The habitats where the lowland subspecies has been taken 6 or 7 times just above the Fall Line, as mapped, are in no way unusual for this form. As a rule, the species inhabits more lowland waters in the north than in the south, much as do many other fishes, including, among Atlantic Coast species, the recently described darter, *Hadropterus notogrammus* (Raney and Hubbs, 1948: 21). The upland subspecies of *N. cummingsae,* however, occurs near the middle of the range of the species and the area of intergradation between the two subspecies appears to disrupt the range of the typical race of *N. c. cummingsae.*

Because of its habitat on the Coastal Plain, *N. cummingsae* has a distribution that usually complements that of the essentially Piedmont


83°
79°
NORTH CAROLINA
SOUTH CAROLINA
35°
35°
NEUSE RIVER
CAPE FEAR RIVER
WACCAMAW RIVER
PEEDEE RIVER
BLACK RIVER
SANTEE RIVER
GEORGIA
ALABAMA
GEORGIA RACE
EDISTO RIVER
COMBAHEE RIVER
CHATTAHOOCHEE RACE
SAVANNAH RIVER
OGEECHEE RIVER
ALTAMAHA RIVER
31°
31°
WESTERN FLORIDA RACE
ST. JOHNS RIVER
ST. MARKS R.
FLORIDA
OCHLOCKONEE RIVER
APALACHICOLA RIVER
PENINSULA RACE
83°
79°

Map 1. Record stations for *Notropis cummingsae* and distribution of the subspecies, intergrades, and races.

All records are original except that for the type locality of *N. c. cummingsae* and all are based on specimens examined. The type localities of the subspecies are indicated by ringed dots. The heavy line approximates the Fall Line (note that only 6 or 7 records of *N. c. cummingsae* lie slightly above the Fall Line). The hachured lines bound the northeastern and southwestern known limits of the range of *N. c. cummingsae* and enclose the inferred ranges of the intergrades and of *N. c. collis*. The races are only provisionally recognized. The figure is based on a section of an outline drainage map of the United States prepared by Walter Johnson and others under the direction of the senior author, as a modification of the United States Geological Survey base map, and printed for the University of Michigan Museum of Zoology in July, 1940. Final drafting of this figure was by Norman J. Wilimovsky, with additions by William L. Cristanelli, Donald B. Sayner, and William L. Brudon. The trivial name has now been emended to *cummingsae*.

species, *N. altipinnis*. In 2 regions, however, the species occur together. In the Neuse River system, where *N. altipinnis* occupies a Coastal Plain habitat, the local subspecies, *N. a. neusensis,* lives with *N. c. cummingsae*. In the upper part of the Santee River system, where *N. cummingsae* takes to the hills, its upland form, *N. c. collis,* occurs with *N. altipinnis wrighti*. In both areas of cohabitation the representatives of the 2 species look surprisingly alike, so much so that some degree of introgressive hybridization (Anderson, 1949) is suggested, though no evidence was found of hybridization or intergradation at the present time. The similarity, however, may merely reflect like responses to the same environment.

SUBSPECIATIONAL PATTERN

Like a number of other southeastern fresh-water fishes, including *Notropis altipinnis* (Hubbs and Raney, 1948), *N. cummingsae* is divisible into subspecies. The pattern of subspeciation, however, contrasts with that of *N. altipinnis*. In harmony with their upland habitats, the local forms of *altipinnis* are stream-system isolates, whereas in *cummingsae* the sharpest segregation is altitudinal. In *altipinnis* the subspecific intergradation involves characters only, for no interbreeding is possible; subspecies status is justified by the inference that differentiation has not become complete. Within *cummingsae,* in contrast, a real intergradation takes place in the lower elevations of the Santee River system, to which the upland subspecies and the intergrades seem to be confined. There is evidence of some altitudinal variation also within the Apalachicola River system, but this differentiation is now interpreted as being below the subspecies level.

The contrast between *cummingsae* and *altipinnis* in respect to geographical variation does not appear to be complete, however, for there are indications of at least racial differentiation between the populations of certain groups of stream systems. Thus, the series from the Neuse to the Combahee, those of the Savannah, the Ogeechee, and the Altamaha, those from peninsular Florida, and the 2 types from the western limits of the species all show average differences that appear more or less definitely to indicate distinct raciation (pp. 12–16).

The pattern of the subspecies now recognized in *Notropis cummingsae* very strikingly parallels the probably subspecific differentiation in *Hadropterus notogrammus,* a percid fish occurring farther north along the Atlantic Coast (Raney and Hubbs, 1948: 20–26, Map 1). Each species has a wide-ranging coastal form, with an upland representative in a single major stream system. In both species the character gradient is in the expected direction. In the darter (*H. notogrammus*) the upland form, as would be expected in a fish of cool swift waters, has an increased number of scales and rays in the vertical fins. In the shiner the number of anal rays decreases in the upland forms following a variational pattern that is exhibited by a number of American cyprinids, notably *Richardsonius* and *Notemigonus* (Hubbs, 1926: 67; Schultz, 1927).

LOWLAND DUSKY SHINER

Notropis cummingsae cummingsae Myers

(Pl. I, Figs. 1–2; Map 1)

Notropis cummingsi.—Myers, 1925: 1–4, Fig. 1 (original description; habitat; associates). Fowler, 1945: 114 (paratype compared with *N. hypselopterus*). Hubbs and Raney, 1948: 7–9 (close resemblance to the Neuse subspecies of *N. altipinnis;* Coastal Plain in Neuse River system).

Cyprinella cummingsi.—Jordan, 1929: 80–82 (compiled).

Hybopsis cummingsi.—Jordan, Evermann, and Clark, 1930: 133. Schrenkeisen, 1938: 138 (compiled).

As indicated in the preceding synonymy, *N. c. cummingsae* has been known only from Myers' description of the type specimens from Burnt Mill Creek, Wilmington, North Carolina; from a brief statement by us, anticipating a conclusion elaborated below; and from some remarks by Fowler, based on a paratype. The other references have been in check lists and manuals, in which the species has been referred to genera into which some recent authors have uncritically divided *Notropis*. This disruption of the genus does not appear to be wise or justified, at least until the whole group has been more thoroughly studied and revised.

The trivial name is emended to *cummingsae* to conform with a recent ruling of the International Commission on Zoological Nomenclature (*Bull. Zool. Nomen.*, 4: 68, 206–7). Myers definitely indicated that the species was "named for Mrs. J. H. Cummings."

Material and Range

We can now show that *N. c. cummingsae* has an extensive range in the Austroriparian region. A total of 3,150 specimens from 93 localities was examined.

List of New Material of Notropis cummingsae cummingsae

The new material of *N. c. cummingsae* includes all that is known except for the single type lot, which has also been examined. Most of the specimens are deposited in the University of Michigan Museum of Zoology and in the Cornell University collections. Others are in the United States National Museum, Charleston Museum, and University of Florida. We have examined all material listed. The locations are all plotted on Map 1. In parentheses are indicated the number of specimens and the range of standard lengths in millimeters. In addition to standard compass directions, with the following "of" deleted, these abbreviations are used: Br. = branch, Co. = county, Cr. = creek, L. = lake, mi. = mile or miles, R. = river, trib. = tributary (of).

Neuse River System, North Carolina.—Wake Co.: Buffalo Cr., 0.5 mi. W. Wendell (1, 38). Wayne Co.: Walnut Cr., 7 mi. WNW. La Grange (6, 38–44); Brooks Swamp, 3.5 mi. N. Mt. Olive (65, 22–51); Nahunta Swamp, 1 mi. N. Pikeville (70, 30–54). Lenoir Co.: Falling Cr., 6 mi. W. Kinston (1, 34); headwaters, Trent R., 1 mi. S. Deep Run (16, 30–54). Craven Co.: tribs. Trent R., 4.5 and 7 mi. WSW. New Bern (25, 34–45). Wilson Co.: Black Cr., 9 mi. N. Fremont (35, 30–54).

Cape Fear River System, North Carolina.—Sampson Co.: trib. Great Coharie R., 4 mi. S. Newton Grove (60, 35–53). Duplin Co.: trib. Northeast Cape Fear R., 1 mi. N. Kenansville (3, 31–35). Cumberland Co.: trib. South R., 1 mi. S. Stedman (10, 28–42); trib. Little Rockfish Cr., 9 mi. W. Fayetteville at State Fish Hatchery (3, 17–39). Bladen Co.: Hammond Cr., trib. Cape Fear R., 1 mi. S. Elizabethtown (66, 18–51). Hoke Co.: tribs. Rockfish Cr., 4.8 mi. NE. Raeford (5, 25–42), and 6 mi. W. Hope Mills (5, 45–51). Harnett Co.: Stuarts Cr., 2 mi. W. Erwin (12, 22–44).

Waccamaw River System, North Carolina.—Columbus Co.: trib. White Marsh, 4 mi. SW. Clarkton (3, 41–42).

Peedee River System, North Carolina and South Carolina.—Moore Co., N. C.: trib. outlet of Aberdeen L., 0.2 mi. S. Aberdeen (98, 25–55). Richmond Co., N. C.: Mark Cr. at Evers Mills (2, 41–44). Scotland Co., N. C.: Drowning Cr., 11 mi. NE. Laurinburg (2, 46–47). Robeson Co, N. C.: Bear Cr., 10 mi. W. Lumberton (4, 40–49). Florence Co., S. C.: Middle Swamp, 3 mi. S. Florence (18, 33–38); Sparrow Swamp, 1 mi. W. Timmonsville (87, 26–50); trib. Jeffreys Cr., 6 mi. SW. Florence (46, 24–54); Jeffreys Cr., 4 mi. W. Florence (34, 22–44). Chesterfield Co., S. C.: trib. Peedee R., 2 mi. NW. Society Hill (96, 22–50). Darlington Co., S. C.: tribs. Peedee R. at Society Hill (57, 28–46) and 11 mi. SW. Society Hill (3, 25–42); trib. Black Cr., 6 mi. NW. Darlington (7, 31–48). Dillon Co., S. C.: Catfish Cr., 1 mi. SW. Latta (125, 29–56). Marlboro Co., S. C.: Beaver Dam Cr., 1.2 mi. NE. McColl (85, 21–60); Whites Cr., 5.5 mi. N. Cherow (1, 50); Crooked Cr., 6 mi. NW. Bennettsville (24, 36–50).

Black River System, South Carolina.—Sumter Co.: 4 mi. W. Sumter (1, 42); trib. Pocotaligo R., 1 mi. W. Sumter (33, 38–49). Sumter–Lee Co. line: Black R., 1 mi. N. Mayesville (27, 29–42). Lee Co.: trib. Black R., 11.3 mi. SW. Bishopville (7, 35–40). Clarendon Co.: tribs. Pocotaligo R. near Alcohe (4, 34–40) and at Manning (2, 38–45); trib. Black R., 2.2 mi. S. Paxville (26, 17–45).

Edisto River System, South Carolina.—Colleton Co.: near Edisto R. at Weeks (Canadys) (15, 37–43). Orangeburg Co.: Goodland Cr., trib. South Edisto R. near Springfield (22, 27–51); tribs. Edisto R. at Branchville (58, 25–49) and 10.3 mi. SW.

Orangeburg (59, 18–57); tribs. Four-Hole Swamp, 5.6 mi. S. Santee (2, 34–40) and 8 mi. S. Santee (35, 23–43). Aiken Co.: Shaws Cr., 4 mi. N. Aiken (18, 30–55).

Combahee River System, South Carolina.—Allendale Co.: trib. Jackson Br., 1.8 mi. S. Sycamore (242, 22–48); trib. Salkehatchie R., 3.4 mi. S. Ulmers (78, 26–52). Barnwell–Bamberg Co. line: trib. Salkehatchie R., 2.6 mi. W. Olar (137, 15–46). Bamberg Co.: trib. Salkehatchie R., 2 mi. S. Olar (138, 19–35).

Savannah River System, South Carolina and Georgia.—Allendale Co., S. C.: tribs. Lower Three Run, 3.6 mi. NW. Appleton (57, 26–43) and 4 mi. NW. Martin (137, 29–48). Richmond Co., Ga.: trib. McBean Cr., 15 mi. S. Augusta, 2 mi. SE. Hepsibah (18, 16–28); Rocky Cr. just below New Savannah Road, about 5 to 8 mi. S. Augusta (38, 24–42); drainage ditch, 4.5 mi. S. Augusta (27, 18–38); trib. Butler Cr., 1 mi. SW. Augusta city limits on U. S. Route 1 (137, 26–43); Boggy Gut Cr., 9 mi. NE. Wrens (90, 20–46); Spirit Cr., 11 mi. SW. Augusta (76, 25–37). Jefferson Co., Ga.: Brushy Cr., 1 mi. S. Wrens (3, 30–44).

Ogeechee River System, Georgia.—Jefferson Co.: Big Cr., 6 mi. S. Wrens (4, 31–40). Burke Co.: Rocky Cr., 9.8 mi. E. Vidette (26, 18–38). Candler Co.: Fifteen Mile Cr., 3.5 mi. W. Pulaski (21, 19–32); Canoochee R., 5 mi. W. Metter (2, 22–23). Bullock Co.: Lotts Cr., 7.4 mi. S. Statesboro (11, 22–32). Hancock Co.: trib. Ogeechee R., 1.7 mi. E. Sparta (4, 37–46). Evans Co.: trib. Canoochee R., 1 mi. NW. Claxton (36, 19–33). Evans–Bryan Co. line: Canoochee R., 2.3 mi. W. Grovel (2, 27–31).

Altamaha River System, Georgia.—Pulaski Co.: Town Cr., trib. Ocmulgee R. at N. limits of Hawkinsville (3, 17–32). Bleckley Co.: trib. Little Ocmulgee R. about 3 mi. E. Cochran (1, 30). Laurens Co.: Rocky Cr., 2 mi. from Bleckley Co. line, near Dudley (17, 23–33); Hunger and Hardship Cr., 5 mi. SW. Dublin (20, 20–33). Emanuel Co.: Ohoopee R. about 15 mi. S. Swainsboro (1, 19); Little Ohoopee R., 9.2 mi. W. Swainsboro (2, 14–27). Greene Co.: Richland Cr., 1.5 mi. W. Greensboro (29, 21–30). Toombs Co.: Swift Cr., 1.5 mi. N. Lyons (6, 17–23); Rocky Cr., 6 mi. SW. Lyons (6, 16–19); trib. Ohoopee R., 3.1 mi. S. Lyons (17, 33–40). Telfair Co.: Little Ocmulgee R., 1.2 mi. N. McRae (6, 22–28). Tatnall Co.: Brazells Cr., 2.3 mi. W. Reidsville (101, 30–46).

St. Johns River System, Northeastern Florida.—Marion Co.: Oklawaha R. at Davenport Landing, about 7 mi. from mouth (8, 19–26); trib. Oklawaha R., 1 mi. W. Orange Springs (6, 19–36). Clay Co.: Clark Cr., 7.3 mi. N. Bostwick (1, 23).

St. Marks River System, Western Florida.—Wakulla Co.: Wakulla R. near Wakulla Springs (4, 20–31).

Ochlockonee River System, Southwestern Georgia.—Grady Co.: trib. Ochlockonee R., 1.6 mi. E. Cairo (131, 19–39); Attapulgus Cr., 3. mi. E. Climax (9, 21–38). Colquitt Co.: Bridge Cr., 4.1 mi. W. Funston (1, 30).

Apalachicola River System, Lower Part, Florida.—Jackson Co.: Spring Cr., 3 mi. SE. Marianna (5, 23–35).

Apalachicola River System (Chattahoochee River Division), Georgia and Alabama.—Harris Co., Ga: Standing Boy Cr., 2.5 mi. SW. Cataula (2, 34–42). Russell Co., Ala.: Watoolee Cr., trib. Uchee Cr., S. Marvyn (1, 39); Brush Cr., trib. Uchee Cr., S. Marvyn (90, 24–43); Uchee Cr. at Marvyn (8, 26–42).

Habitat

This shiner inhabits various types of streams on the Coastal Plain. It is not confined to swift unstained waters like those of Burnt Mill Creek where the types were secured (Myers, 1925: 3). Some specimens were seined over sand and gravel on riffles, but most were secured over silt-covered detritus and sand in quiet waters or in schools below trailing aquatic weeds in moving water. The color of water was noted as slightly brownish to almost black. Aquatic vegetation grew at some of the collecting stations. Like most other kinds of *Notropis, N. c. cummingsae* is gregarious. It is often seen in schools of more than 100 individuals.

Relationships

In the maze of species groups that constitute *Notropis* the relationships of *N. cummingsae* are not very obvious. In general appearance it simulates *N. altipinnis,* with which it is compared below, and other kinds having 2, 4—4, 2 teeth, but Myers gave the dental formula as 1, 4—4, 1. For 57 specimens taken throughout its range we count (from left to right): 1, 4—4, 1 in 50; 0, 4—4, 1 in 3; 1, 4—4, 0 in 3; and 1, 4—3, 0 in 1 (the one with only 3 teeth on the right side, a most unusual number, shows no sign of a missing alveolus or gap, and the 3 teeth are sufficiently broad-based to fill the dentigerous space). There is little similarity in specific characters between this species and any previously described form having 1, 4—4, 1 as the usual tooth complement.

Most shiners that have a definite blackish band like that of *cummingsae* differ in having 2, 4—4, 2 teeth. The several species of the *N. hypselopterus* group, which agree with *cummingsae* in having a broad dark lateral stripe, differ in having considerable dark pigment on the dorsal and anal fin membranes; they also differ in many other respects. Contrary to the statements usually seen in the literature, the members of the *hypselopterus* group have been found by Royal D. Suttkus to have the teeth normally 2, 4—4, 2, and occasionally 1, 4—4, 1. Fowler (1945: 114) compared *cummingsae* only with *N. hypselopterus* (Günther), but these species are neither similar in appearance nor close in relationship.

In the typical number (10 or 11) of anal rays (Table I), *N. c. cummingsae* differs sharply from the black-striped shiners with 4—4 teeth, such as *N. alborus* Hubbs and Raney (1947), which has 7 anal rays. The high number of anal rays likewise distinguishes *N. c. cummingsae* from *N. chalybaea* (Cope), which usually has 8 anal rays and 2, 4—4, 2 teeth, and from *N. petersoni* Fowler (1942: 1–2, Figs. 1–2), which has 7 anal rays and either 1 or 2 teeth in the lesser row. Two nominal species that we surmise are synonyms of *N. petersoni,* namely *N. norrisi* Fowler (1945: 235, Figs. 114–16) and *N. williami* Fowler (1945: 236, Figs. 117–19), were described as having a dark lateral stripe and as having the teeth, respectively, 1?, 4–4, 1? and 1, 4–4, 1, and the anal rays only ii, 6 or ii, 7 and iii, 6 (presumably equivalent to 7 or 8, and 7 principal rays).

N. cummingsae collis, which usually has 9 anal rays, differs less sharply in this one respect from the species mentioned.

Notropis c. cummingsae differs otherwise from *N. chalybaea,* with which it often occurs. The distal margin of the anal fin is distinctly instead of scarcely concave. The other fins are more rounded. The fins are all shorter and the height of the dorsal is less than the head length, rather than being equal to or greater than that measurement. The dorsal origin is nearer to the caudal base than to the tip of the snout, rather than equidistant between those points or, as is usual, nearer the snout tip. The lateral stripe is broader, is less sharply limited below, and passes well below the lateral line at its lowest extent. The narrower and usually blacker stripe of *chalybaea,* in contrast, is sharply delimited and passes below the lateral line only where the black specks cluster about the lateral-line pores. The basicaudal spot of *cummingsae,* instead of ending abruptly, streaks backward on the membranes. On the opercle the stripe extends well below the middle in *cummingsae* but is limited to the upper half in *chalybaea.* The breast and the belly are immaculate or have few small scattered chromatophores, whereas in *chalybaea* these parts have many large melanophores. The underside of the caudal peduncle bears few scattered chromatophores, rather than numerous conspicuous specks that are more or less continuous in 2 lines on the anterior two-thirds of the peduncle.

Notropis cummingsae is probably most intimately related to *N. ortenburgeri* Hubbs, a species of western Arkansas and eastern Oklahoma (Hubbs, in Ortenburger and Hubbs, 1927: 127; Hubbs and Ortenburger, 1929: 72–73). The two agree closely in size, pigmentation, physiognomy, proportions, and ray counts. The most notable difference is in dentition, for *ortenburgeri* consistently has only 4–4 teeth. In this respect it departs further from expectation than does *cummingsae,* for nearly all species of *Notropis* with the external characters of *cummingsae* and *ortenburgeri* have 2, 4–4, 2 teeth. Within the *Notropis* complex such indications of relationship minimize the probable taxonomic significance of the number of teeth in the lesser row.

Comparison with Notropis altipinnis

In many respects *N. c. cummingsae* agrees closely with *N. altipinnis* (for synonymy, characters, and range see Hubbs, 1941, and Hubbs and Raney, 1948). In general coloration and in number of anal rays they are very similar. Attention to detail, however, brings out numerous differentiae in addition to the dental distinction already indicated.

Some of the best differences are in mouth structure. The gape is less oblique in *cummingsae* than in *altipinnis.* The upper lip averages thicker and is hooked slightly downward anteriorly. The lower jaw is not hooked upward as it is, more or less, in *altipinnis.* As seen from the front, the mouth is more broadly U-shaped. These distinctions are not very striking, though they are still evident, at least on the average, when the Neuse River race of *N. altipinnis (neusensis)* is compared with *N. cummingsae.* The angle between the edge of the premaxillary and the top of the head, which in 35 adults of *N. c. cummingsae* varies from 45° to 62°, with an average of 56°, is generally less than in most forms of *N. altipinnis* (Hubbs and Raney, 1948: 9).

The fins are usually shorter and more rounded in *N. c. cummingsae* than in *N. altipinnis. N. a. neusensis,* however, differs little from *cummingsae* in this respect. For this character the sexes should be compared separately because in both species, as is usual in minnows, the males have higher and sharper fins than do the females.

The nuptial tubercles are coarser in *N. c. cummingsae* than in *N. altipinnis* and are differently arranged. The distinctions will be appreciated on comparing the following description of the tubercles in *cummingsae* with the detailed account of these structures in *altipinnis* (Hubbs, 1941: 171). In *N. c. cummingsae* the tubercles are enlarged on the muzzle, especially in a definite row along the edge of the snout. Those on the mandible are also somewhat enlarged. The largest mandibular tubercles, pointing somewhat outward, border the outer edge of each ramus. On the pectoral rays they are uniserial toward the extreme base, elsewhere biserial. In each series there are about 3 pointed tubercles on each ray segment. Minute tubercles are scattered along the dorsal and pelvic rays, often several per segment.

The lateral band is wider in *N. c. cummingsae* than in *N. altipinnis.* It covers most of the opercle and extends as a solid band below the lowest part of the lateral line. In *altipinnis,* in contrast, the band is restricted to the upper half of the opercle and extends below the lateral line only where melanophores are clustered about the lateral-line pores. In the more typical races of *altipinnis* the band does not even reach the lateral line where it is arched downward.

The pigmentation on the top of the head is less variegated than in *N. altipinnis,* and the snout is lighter in the ring adjoining the nostrils. *N. c. cummingsae* lacks the dark blotch that is developed on the middle of the front of the snout in *altipinnis. N. a. neusensis,* however, approaches *N. c. cummingsae* in this character also, but the distinction is not obliterated.

There are also differences in the detailed pigmentation of the body. The median predorsal dark streak is rather well developed in *N. c. cummingsae* but is weak to obsolete in *N. altipinnis.* The lower edge of the caudal peduncle bears a number of scattered melanophores in *N. c. cummingsae* but usually few to none in *N. altipinnis.* This distinction largely breaks down in the Neuse River system. The region about the front of the anal fin and about the anus is deeply charged with black pigment in *N. c. cummingsae* instead of being nearly or quite clear. In this feature, too, *N. altipinnis neusensis* approaches *N. c. cummingsae* but remains separable.

It will be clear from the foregoing comparison that the Coastal Plain form, *N. c. cummingsae,* differs sharply and very obviously from the essentially Piedmont species, *N. altipinnis,* but that the distinction is impaired in the Neuse River system, where *N. a. neusensis* occurs on the Coastal Plain in company with *N. c. cummingsae.* The 2 species also show superficial similarity where a subspecies of *N. cummingsae (collis)* lives with *N. altipinnis wrighti* in the uplands of the Santee River system. The differentiation in external features is not completely broken down, however, and all specimens of *cummingsae* and *altipinnis* in the restricted areas of joint occurrence are separable on close scrutiny. Their specific rather than subspecific separation is therefore indicated. The diagnosis based on characters of pigment and form is confirmed by an examination of the pharyngeal teeth, for the aberrant subspecies of *altipinnis* in the Neuse system retains the dental formula 2, 4–4, 2, and *N. c. collis* has 1, 4–4, 1 teeth.

Other Characters

Notropis c. cummingsae is a small shiner, rarely if ever attaining a total length of 3 inches. The largest of the 3150 specimens examined is only 60 mm. in standard length.

Proportional measurements, taken to correspond with those given by Hubbs (1941) for *N. altipinnis* and *N. scepticus* and by Hubbs and Raney (1948) for the subspecies of *N. altipinnis,* are given in Table IV. Fin rays in 20 specimens from various localities are: dorsal, 8 in all; pectoral, 14–14 to 16–16 (average 14.6); pelvic, 8–8 (rarely 7–7 or 9–9, less rarely 8–9 or 9–8). Anal ray counts are detailed in Tables II and III.

TABLE I

FREQUENCY DISTRIBUTION OF LARGEST SPECIMEN IN EACH COLLECTION OF NOTROPIS CUMMINGSAE

Subspecies and Race	Standard Length in mm.				
	15–24	25–34	35–44	45–54	55–64
Notropis c. cummingsae					
Carolina	..	5	24	21	2
Georgia	4	12	9	4	..
Peninsular	1	1	1	..	..
Western Florida	..	2	3	..	..
Chattahoochee	..	..	4	..	..
Intergrades	..	2	2	3	..
Notropis c. collis	..	1	3	..	..

The nuptial colors, as indicated by a specimen taken in Alabama on May 10, 1939, and examined after 14 days in formalin, are only moderately bright. There is some pale orange on the caudal lobes and a trace of orange on the dorsal rays. The back is waxy green, with a deep-lying wash of pale orange just above the dark stripe. The blackish lateral stripe and the adjacent parts of the silvery white lower trunk are washed with purplish rose. In live specimens from North Carolina, the dark lateral stripe is greenish and is paralleled above by a narrow orange stripe.

Females average larger and stouter than males. The collection from Rocky Creek, near Augusta, Georgia, taken April 27, 1941, contained 16 nuptial males 30 to 38 mm. in standard length, averaging 34.1 mm., and 20 gravid females 32 to 42 mm. long, averaging 37.0 mm.

Geographical Variation

Even after the separation of the upland subspecies, *N. c. collis,* described below, *N. c. cummingsae* remains a complex of local forms, most or all of which are probably genetic races. Some of these stocks may warrant subspecific separation after the rich cyprinid fauna of the southeast has been subjected to more critical study. Five such races are provisionally recognized:

CAROLINA RACE.—In the stream systems from the Neuse in North Carolina to the Combahee in South Carolina, *N. cummingsae* is characterized by the comparatively large size attained (Table I), the high average number of anal rays (Tables II and III), and the relatively robust build and dark color (Pl. I, Figs. 1–2). The largest specimen in each collection is nearly always more than 34 mm. long (standard length) and is usually 45 to 54 mm. long in a series of 5 or more specimens. The anal rays frequently number 11, occasionally 12, with a grand average of 10.28 and with means for stream systems ranging from about 10.3 to 10.4, except in the Edisto Basin. The specimens from that stream system, next to the southernmost in the range of this race, almost equal those from the Georgia streams in having an average of only 10.12 anal rays, but in size and appearance they more closely resemble the examples from streams farther north.

GEORGIA RACE.—The 897 specimens from the Savannah, Ogeechee, and Altamaha river systems in Georgia are smaller on the average than

TABLE II

NUMBER OF ANAL RAYS IN NOTROPIS CUMMINGSAE

Consistency within certain stream systems is indicated in Table III.

Subspecies, Race, and Stream System	Number of Anal Rays							
	8	9	10	11	12	No.	Mean	SE
N. c. cummingsae	1	193	2102	815	39	3150	10.22	.01
Carolina race	1	96	1260	597	33	1987	10.28	.01
Neuse River	..	5	134	75	4	218	10.36	.04
Cape Fear River	..	6	94	67	6	173	10.42	.05
Waccamaw River	..	..	2	1	..	3	10.33?	..
Peedee River	..	49	431	195	14	689	10.25	.02
Black River	..	1	56	41	2	100	10.44	.06
Edisto River	1	12	157	38	1	209	10.12	.03
Combahee River	..	23	386	180	6	595	10.28	.02
Georgia race	..	72	676	147	2	897	10.09	.02
Savannah River	..	49	449	84	1	583	10.06	.02
Ogeechee River	..	10	77	18	1	106	10.09	.05
Altamaha River	..	13	150	45	..	208	10.15	.03
Peninsular race								
St. Johns River	..	1	12	2	..	15	10.07	.12
Western Florida race ...	..	6	75	65	4	150	10.45	.03
St. Marks River	..	..	1	3	..	4	10.75?	..
Ochlockonee River ..	..	6	71	60	4	141	10.44	.05
Lower Apalachicola R.	..	..	3	2	..	5	10.40?	..
Chattahoochee race								
Chattahoochee River ..	..	18	79	4	..	101	9.86	.04
All races except Chattahoochee	1	175	2023	811	39	3049	10.23	.01
Intergrades								
Santee River System ..	..	28	40	5	..	73	9.68	.07
6 small collections ...	..	5	4	1	..	10	9.60	.22
2.8 miles W. Summerton	..	23	36	4	..	63	9.70	.07
N. c. collis	1	30	3	..	..	34	9.06	.06
Grand total for species	2	251	2145	820	39	3257	10.20	.01

the Carolina specimens (Table I). They are relatively frailer, deeper bodied, and usually paler than examples of the Carolina race. Since nearly all this material came from the Tifton Upland, where most of the streams are relatively clear and sandy, the small size, wafery build, and palish color may be, in part at least, the direct imprint of the environment. The anal rays are seldom 11 and average 10.09.

On the basis of the anal ray counts alone a subspecific separation of the Carolina and Georgia races is not admissable. On the basis of other characters, such as size, deepness of pigmentation, and general fragility, a subspecies separation might appear warranted, should it appear highly probable that these differences are genetic.

Peninsular race.—In their small size, large eyes, fragile structure, and in their low average number (10.07) of anal rays, the 15 specimens from the St. Johns River system in Florida resemble the Georgia stocks, but differ in being very dark and in having dark flecks on the lower sides (perhaps a purely environmental response). The large melanophores that are scattered over the peritoneum of all the races show through the body wall in the Florida specimens.

Western florida race.—The 150 specimens from the St. Marks and lower Apalachicola river systems in western Florida and from the Ochlockonee River system in southwestern Georgia, just north of western Florida, seem to be intermediate between the Georgia and Carolina races in size (Table I) and general appearance, but have the anal rays at least as numerous, on the average (10.45), as in the Carolina stocks. They have none of the characteristics of the Chattahoochee race. Material is inadequate to show whether the forms in the St. Marks and the lower Apalachicola river systems differ from the Ochlockonee type, which alone is well represented by specimens.

Chattahoochee race.—Most distinctive among the races left in *N. c. cummingsae* is one represented by 3 series from the basin of Uchee Creek, eastern Alabama, and by 1 series from Standing Boy Creek, Georgia, all in the Fall Line Hills section (Fenneman, 1938: 67, Fig. 21) of the Chattahoochee River division of the Apalachicola River system. The specimens of this race have on the average a deeper and thicker body and a deeper caudal peduncle than do those from other stream systems. They also show a reduced average number of anal rays (Table II). In this respect they approach *N. c. collis,* no doubt as the result of independent variation. There are also suggestions of aberrancy in other proportional measurements (Table IV). It is not certain, however, that the robust body and other differential propor-

TABLE III

RELATIVE STABILITY IN NUMBERS OF ANAL RAYS OF NOTROPIS C. CUMMINGSAE WITHIN CERTAIN STREAM SYSTEMS

Localities are specified in more detail on pages 6–7. Counts for small series are deleted from this table but are included in the compilations in Table II.

Race, River System, and Locality	Number of Anal Rays							
	8	9	10	11	12	No.	Mean	SE
Carolina race								
Neuse River System, N.C.								
Trent River tributaries	..	..	25	15	..	40	10.37	.10
Brooks Swamp	..	3	37	25	..	65	10.34	.07
Nahunta Swamp	..	1	40	26	3	70	10.44	.07
Black Creek	..	1	24	9	1	35	10.29	.10
Cape Fear River System								
Trib. of Great Coharie R.	..	2	32	25	1	60	10.42	.08
Hammond Creek	..	3	41	20	2	66	10.32	.08
Peedee River System								
Outlet of Aberdeen L.	..	7	64	25	2	98	10.22	.06
Sparrow Swamp	..	6	57	19	5	87	10.26	.07
Trib. of Jeffreys Creek	..	3	26	16	1	46	10.33	.09
Jeffreys Creek	..	4	18	11	1	34	10.26	.12
Tribs. of Peedee River								
NW. of Society Hill	..	4	58	34	..	96	10.31	.06
At Society Hill	..	2	41	14	..	57	10.21	.06
Catfish Creek	..	11	80	33	1	125	10.19	.05
Beaver Dam Creek	..	7	50	25	3	85	10.28	.07
Black River System								
Trib. of Pocotaligo R., Sumter County	..	1	17	15	..	33	10.42	.10
Black River	..	..	17	8	2	27	10.44	.12
Trib. of Black River, Clarendon County	..	..	14	12	..	26	10.46	.10
Edisto River System								
Tribs. of Edisto River At Branchville	..	4	43	11	..	58	10.12	.07
Trib. of Edisto River SW. of Orangeburg	..	2	44	12	1	59	10.20	.07
Trib. of Four-Hole Swamp	1	5	22	7	..	35	10.00	.12
Combahee River System								
Trib. of Jackson Br.	..	15	163	60	4	242	10.22	.04
Tribs. of Salkehatchie R.								
South of Ulmers	..	3	47	28	..	78	10.32	.06
West of Olar	..	3	88	45	1	137	10.32	.04
South of Olar	..	2	88	47	1	138	10.34	.04
Georgia race								
Savannah River System								
Tribs. of Lower Three-Run								
Near Martin	..	3	104	29	1	137	10.20	.04
Near Appleton	..	3	46	8	..	57	10.09	.06
Spirit Creek	..	4	55	17	..	76	10.17	.06
Boggy Gut Creek	..	11	65	14	..	90	10.03	.05
Trib. of Butler Creek	..	18	107	12	..	137	9.96	.04
Trib. of McBean Creek	..	6	65	11	..	82	10.06	.05
Rocky Creek	..	8	27	3	..	38	9.87	.09
Ditch near Augusta	..	1	26	..	..	27	9.96	.04
Ogeechee River System								
Trib. of Canoochee R.	..	3	28	4	1	36	10.08	.09
Rocky Creek	..	1	21	4	..	26	10.12	.08

tions are of racial rather than direct environmental basis. Were it not for this doubt, we would probably describe this race as another distinct subspecies.

The geographical variation in the average number of anal rays (Tables II and III) seems to have an environmental correlation even within *N. c. cummingsae.* Toward the western limits of the species, for example, there seems to be a marked upstream reduction in the average number (from 10.45 to 9.86), which parallels the distinction between the lowland Carolina race (averages from 10.12 to 10.44) and the upland subspecies, *N. c. collis* (average 9.06). In correlation with the slight reduction in the average number of anal rays in the sandy waters of the Savannah and Altamaha systems, these streams are of a more upland and presumably of a cooler type than are those of the Carolina lowlands. In fact, most of the collections of this race have come from a slightly elevated region that has been named the Tifton Upland (Fenneman, 1938: 40–42, 68, 77–79, 118, Figs. 15, 21; Pl. 3). The 15 specimens from the St. Johns River system in Florida yield an average of only 10.07 rays, and it may be significant that the stream in which most specimens were taken, the Oklawaha River, originates in a giant spring. Within stream systems from North Carolina to Georgia, below the Fall Line, the number of rays is rather constant (Table III).

The most obvious geographical variant in the species, the upland form of the Santee River system of South Carolina and North Carolina, obviously warrants subspecific separation and is defined as:

UPLAND DUSKY SHINER

Notropis cummingsae collis, new subspecies

(Plate I, Fig. 3; Map 1)

The type material comprises 34 specimens from 5 localities. In addition, 73 examples in 7 collections are regarded as intergrades, *Notropis cummingsae: collis* × *cummingsae.* All known material is deposited in the University of Michigan Museum of Zoology (UMMZ), Cornell University (CU), and the Charleston Museum (CM). In the following lists of specimens the same abbreviations are used as in the list of material of *N. c. cummingsae.*

TYPE SPECIMENS.—The holotype, UMMZ No. 160557, an adult female 34 mm. in standard length, was collected by Elmer E. Brown on September 6, 1946, in Roses Creek, a small stream in the Catawba River system, 1.5 mi. S. of Smyrna on State Highway 181, Burke Co., North Carolina. The 5 paratypes, UMMZ 160558 (2), and CU 11218

(3), 30 to 36 mm. long, are from same locality (ringed on Map 1). The additional paratypes bear the following data: UMMZ 94556–57 (18, 25–43 mm.), Donald J. Ameel, Nov. 11, 1931, creek in Santee R. system (trib. to either Catawba R. or Broad R.), near York, York Co., S. C.; UMMZ 94553 (1, 27), Ameel, Nov. 11, 1931, Steele Creek, Catawba R. system, near Rock Hill, York Co., S. C.; CU 11269 (9, 29–37), Brown, Aug. 13, 1946, South Fork Cr., Catawba R. system, between Rock Hill and Chester, Highway 21, Chester Co., S. C.

DATA ON INTERGRADES, *Notropis cummingsae: collis × cummingsae,* ALL FROM THE LOWER SANTEE RIVER SYSTEM, SOUTH CAROLINA.—UMMZ 143214 (1, 31 mm.), E. Milby Burton, Aug. 18, 1931, Beaver Dam Cr., trib. Saluda R., 5 mi. from Newberry on the Newberry–Saluda Road, Newberry Co. CU 11270 (3, 42–48), Harry W. Freeman, June 17, 1947, North Br. Crane Cr., 12 mi. N. Columbia, Richland Co. CU 11271 (1, 47), Freeman, Aug. 1, 1947, Twenty Five Mile Cr., near Blythewood, Richland Co. UMMZ 143247 (2, 26–27) and 1 returned to CM, Burton, Aug. 19, 1931, Millwood Pond, St. Matthews, Calhoun Co. Collected by R. D. Suttkus and parties, 1949, as follows: CU 15295 (1, 44), June 8, Congaree Cr., 2.5 mi. SSW. Cayce, Lexington Co.; CU 15245 (1, 37), June 8, Congaree Cr., 0.6 mi. farther south; CU 18417 (63, 17–45), Dec. 27, trib. Santee R., 2.8 mi. W. Summerton, Clarendon Co.

DISTRIBUTION AND HABITAT.—*Notropis cummingsae collis* is known only from the Piedmont and Mountain streams of the Santee River system in South Carolina and North Carolina (Map 1). It is probably of wide occurrence throughout these waters, but there is no evidence of its living in any other stream system. Three of the 4 record stations are in the Catawba River division of the Santee complex and the fourth is from either that division or from the Broad River branch. Though provisionally placed in the supposed area of intergradation, a station in the Saluda River division may pertain to *collis* (the single specimen, like *collis*, has 9 anal rays, but the intergrades have about an even chance of having that number). The probable occurrence of an intergrade in the Saluda branch suggests that *N. c. collis* occurs farther upstream in that branch. Assuming that it does occur there, we tentatively map the range of that subspecies as the entire upland part of the Santee River system.

The limited data suggest that *N. c. collis* inhabits small, more or less clear streams, with slow to moderate current and with sandy bottom partly covered with fine sediment.

Diagnosis and status.—This small form of *Notropis* is essentially like *N. c. cummingsae* in dentition (1, 4–4, 1) and in other characters, but usually has 9 rather than 10 or 11 principal anal rays. Subspecific status is indicated by the overlap in anal ray counts and in other characters and, especially, by the areal intergradation.

Intergradation.—Series interpreted as intergrades between the upland form, *N. c. collis,* and the wide-spread lowland form, *N. c. cummingsae,* have been taken in the Santee River system near and below the Fall Line (Map 1). Unfortunately, only 7 series can be so identified and, with the exception of one set of 63 fish, they each comprise only 1 to 3 specimens. Since the main distinction involves only 1 anal ray and since the intergrades should have either 9 rays as in *collis* or 10 as in typical *cummingsae,* the identification of single specimens is rather arbitrary and the allocation of small samples is insecure. Large series are needed to establish beyond doubt the intermediacy of the stock at each locality and to delimit more precisely the area of intergradation.

That the 2 forms intergrade, rather than overlap without fusion, is definitely indicated by the characters of the one adequate series, which came from the station of lowest elevation. In this series, which is essentially uniform in its characters, the anal rays average 9.70. In the 6 smaller series regarded as intergrades, the mean is 9.60. Both values are intermediate between the average for typical *collis* (9.06) and the means for the river systems on either side of the Santee, namely 10.44 for the Black and 10.12 for the Edisto. Since the smaller series of putative intergrades are relatively uniform in appearance and stem from a small region where intergradation is expected, we feel little doubt in our inference that *collis* and *cummingsae* intergrade not only below but also near the Fall Line.

It is probable that the area of intergradation extends throughout the lower Santee River system, splitting the range of *N. c. cummingsae.* Downstream dispersal of *collis* into a lowland area formerly inhabited by the nominate subspecies probably produced this pattern of intergradation.

The anal ray counts for the 7 series identified as intergrades are: UMMZ, No. 143214–9(1); CU, No. 11270–9(1), 10(2); CU, No. 11271–10(1); UMMZ, No. 143247, and CM–9(2), 10(1); CU, No. 15295–11 (1); CU, No. 15245–9(1); CU, No. 18417–9(23), 10(36), 11 (4).

A trend toward intergradation may be shown by the specimens from the southernmost station mapped for *N. c. collis.* Of the 9 specimens, 7 have 9 anal rays and 2 have 10. In the 25 other specimens referred to *N. c. collis* the only variation from 9 anal rays is in one series (UMMZ, 94556–57), in which the counts are: 8(1), 9(16), 10(1).

Comparison with *N. c. cummingsae*.—In *N. c. collis* the number of anal rays is typically 9, rarely 8 or 10, whereas in *N. c. cummingsae* the number is usually 10, often 11 (especially in the typical Carolina race), rarely 8 or 12 (Table II). The 9 paratypes of *N. cummingsae* examined have 9 rays in 1, 10 in 4, and 11 in 4. The number in *N. c. cummingsae* (Tables II and III) is rather consistent and shows a slightly confusing and presumably independent approach toward the reduced number of *N. c. collis* in the Chattahoochee race (possibly a subspecies), which is otherwise aberrant (p. 14). When we exclude that race and the intergrades and draw the line of distinction between 9 and 10 anal rays, we find that 94 per cent of the specimens of *N. c. cummingsae* are separable from 91 per cent of known examples of *N. c. collis*. This difference alone seems sufficient to warrant subspecific separation. The low number of anal rays is reflected in the reduced length of the anal base (Table IV).

Long comparison reveals few other distinctions and none as trenchant or as trustworthily genetic as the difference in the number of anal rays and the length of the anal base. Most proportional measurements are similar (Table IV). The body averages a little deeper and wider than in the typical Carolina race of *N. c. cummingsae,* but less deep and less wide than in the Chattahoochee race. The caudal peduncle averages slightly longer, but the overlap is very wide. The interorbital averages wider. The dorsal averages a little higher. *N. c. collis* may average somewhat smaller than the typical or Carolina race of *N. c. cummingsae,* for the largest specimens of the 2 forms are 43 and 60 mm. in standard length, respectively, and the largest specimen in almost half the lots of the Carolina race of *cummingsae* is more than 43 mm. long (Table I). The upland form *(collis),* however, averages larger than the Georgia race of the lowland subspecies.

As a rule, *N. c. collis* is less dusky than typical *N. c. cummingsae* (Pl. 1). The difference is particularly noticeable on the top of the head and on the snout. In *N. c. collis* relatively few melanophores cross the front of the clear light streak that rings the snout from eye to eye, passing through the nostrils, whereas in typical *N. c. cummingsae* the light ring is more or less disrupted anteriorly by a darkish bar. In *N. c. collis* the light triangle just above and behind the eye, as well as the light dash that connects this mark with the pale streak above the dark lateral band of the body, is typically clearer of dark pigment and, therefore, more conspicuously light. In *N. c. collis* the sides below the

TABLE IV

MEASUREMENTS OF NOTROPIS CUMMINGSAE IN THOUSANDTHS OF STANDARD LENGTH

Under each series there is given for each character the range of variation and, in parentheses, the average. Under *collis*, the bold-face figure in each second row is the value for the holotype. For methods of measuring see Hubbs and Lagler (1941 and 1947).

Subspecies	*Notropis cummingsae cummingsae*						*N. c. collis*
Race	Carolina				Chatta-hoochee	Both	
Stream System	Neuse	Cape Fear	Peedee	Edisto	Chatta-hoochee	All 5	Santee
State	N. C.	N. C.	S. C.	S. C.	Ala.	N.C.–Ala.	N.C.,S.C.
Stream	Walnut Cr. & Trent R.	Hammond Cr. & trib. South R.	Crooked Cr.	Trib. near Edisto R.	Brush Cr.	All Streams	All Streams
Number of specimens	8	8	8	7	8	39	9
Standard length, mm.	39–49 (44.3)	39–49 (41.5)	35–50 (39.7)	35–42 (38.6)	34–41 (38.4)	34–49 (40.6)	33–42 **34**(36.4)
Predorsal length	511–555 (539)	520–555 (538)	525–556 (541)	536–567 (548)	492–546 (528)	492–567 (538)	508–562 **530**(537)
Dorsal to occiput	338–361 (352)	319–353 (340)	307–353 (334)	323–354 (342)	308–339 (327)	307–361 (339)	325–361 **325**(340)
Prepelvic length	477–497 (487)	472–504 (486)	470–500 (482)	474–500 (489)	472–512 (492)	472–512 (487)	474–505 **479**(491)
Body depth	181–209 (196)	183–242 (208)	203–249 (220)	216–229 (221)	226–244 (235)	181–249 (216)	209–243 **222**(224)
Body width	103–128 (116)	106–143 (120)	102–131 (118)	116–135 (128)	143–166 (152)	102–166 (127)	117–151 **124**(134)

Caudal peduncle depth	84–96 (89)	85–105 (94)	88–101 (96)	90–106 (98)	101–118 (106)	84–118 (97)	96–104 **98**(100)
Caudal peduncle length	209–236 (225)	202–257 (218)	200–242 (212)	186–212 (201)	201–228 (217)	186–257 (215)	206–251 **231**(230)
Head length	236–251 (244)	236–252 (245)	237–254 (246)	243–253 (248)	241–261 (250)	236–261 (247)	236–258 **249**(251)
Head depth	146–164 (157)	149–163 (157)	152–168 (160)	156–164 (160)	164–176 (167)	146–176 (160)	155–175 **163**(167)
Snout length	68–73 (71)	69–79 (73)	67–76 (72)	64–74 (70)	65–76 (71)	64–79 (71)	66–82 **77** (76)
Eye length	72–81 (77)	73–86 (80)	77–87 (85)	75–85 (81)	78–89 (85)	72–89 (82)	79–89 **89** (85)
Interorbital, least fleshy width	78–89 (84)	84–93 (89)	82–95 (88)	83–93 (86)	84–89 (86)	78–95 (87)	91–100 **95** (98)
Upper jaw length	77–91 (82)	73–86 (79)	72–85 (78)	78–85 (81)	76–89 (83)	72–91 (81)	71–92 **80** (83)
Dorsal origin to lateral line	124–145 (135)	117–155 (134)	141–155 (147)	128–147 (141)	150–173 (158)	117–173 (143)	138–165 **142**(150)
Pelvic insertion to lateral line	47–70 (61)	57–99 (74)	62–93 (77)	67–93 (83)	89–100 (94)	47–100 (78)	78–97 **92** (88)
Dorsal height	224–268 (241)	217–269 (246)	231–268 (251)	215–241 (233)	221–269 (238)	215–269 (242)	229–273 **246**(246)
Anal height	194–221 (208)	191–233 (209)	192–229 (208)	181–229 (201)	175–208 (195)	175–233 (204)	185–218 **198**(201)
Anal base	134–181 (158)	143–181 (157)	145–192 (170)	156–167 (162)	143–167 (152)	134–192 (160)	125–147 **136**(133)
Pectoral length	176–209 (191)	179–234 (198)	182–209 (201)	181–221 (194)	191–223 (200)	176–234 (197)	185–221 **204**(199)
Pelvic length	149–190 (165)	139–188 (164)	154–198 (176)	141–184 (162)	149–187 (160)	139–198 (166)	147–184 **154**(161)

lateral band are immaculate, with few or no melanophores, whereas in *N. c. cummingsae* black specks frequently encroach from above into this light area.

RAY AND SCALE COUNTS IN HOLOTYPE (AND PARATYPES).—Dorsal, 8 (7 in 2, 8 in 28). Anal, 9 (all counts in Table II). Caudal, 19, consistently. Pectorals, 14—14 (usually 14—14, occasionally 13—14, 14—13, or 13—13). Pelvic, 7—8 (7—7 in 1, 7—8 in 4, 8—7 in 1, and 8—8 in 25). Scales 6 (5 to 7, usually 6)—37 (35 to 37, most frequently 36, often 37)—4 (3 to 4, usually 4).

SUMMARY

The dusky shiner, *Notropis cummingsae* Myers, has previously been known only from the type locality in North Carolina, but is now reported from more than 100 other localities, ranging from the Neuse River system in east-central North Carolina to the Apalachicola system in southwestern Georgia, western Florida, and southeastern Alabama. Like many other fishes, it largely avoids the Florida peninsula. As a rule it seems to select more lowland habitats toward the north, as do many other fishes. With one notable exception, its populations are characteristic of the Austroriparian region and of the Coastal Plain. It closely resembles the essentially Piedmont species, *N. altipinnis,* and these species are usually complementary in distribution. Probably as a result of parallel speciation rather than of introgressive hybridization, they are confusingly alike in the 2 areas where they occur together—in the Neuse River system, where *N. altipinnis* is represented by the lowland subspecies *N. a. neusensis,* and in the upper Santee system, which is jointly occupied by the new upland subspecies *N. cummingsae collis* and by *N. altipinnis wrighti.* Even in these areas of cohabitation, however, the 2 species are consistently distinguishable, particularly in details of pigmentation. Furthermore, they differ trenchantly in tooth formula and show no sign of intergradation. Unlike *altipinnis* and other species of similar appearance, *cummingsae* has only 1 tooth in the outer row. It is probably most closely related to *N. ortenburgeri,* of Arkansas and Oklahoma, which is still more aberrant among shiners of this type in the complete lack of the outer row of teeth.

The pattern of subspeciation in *N. cummingsae,* strikingly like that of *Hadropterus notogrammus,* is featured by relative uniformity in the lowlands, by a subspecific segregate in the Piedmont and Mountain districts of a single stream system (that of the Santee River), and by intergradation near and below the Fall Line. The intergrades occupy the lower Santee River system and appear to split the range of *N. c. cummingsae.* Downstream dispersal and hybridization seem to have caused this pattern of intergradation. There is evidence of altitudinal differentiation also in the Apalachicola River system. The Chattahoochee race, living in the Fall Line Hills, is perhaps also worthy of subspecific separation. In addition to this race and *N. c. collis,* 4 lowland races of *N. c. cummingsae* are tentatively recognized, namely the Carolina race, the Georgia race, the Peninsular race, and the Western Florida race.

In line with a general trend among American cyprinids there seems to be a negative correlation between the number of anal rays on the one hand and the altitude and the water temperature on the other. In the Carolinas the anal rays average about 10.1 to 10.4 in the populations of *N. c. cummingsae* and 9.06 in the upland subspecies, *N. c. collis.* In the Apalachicola and adjacent river systems the averages are 10.45 for the lower elevations and 9.86 for the Fall Line Hills. The Georgia race, chiefly from the Tifton Upland, has on the average 10.09 anal rays and, as a rule, inhabits waters of a more upland type and presumably of cooler temperatures than does the Carolina race. The Peninsular race, largely from a stream originating in a huge spring, has 10.07 anal rays as the mean.

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Submitted for publication February 20, 1951

PLATE I

Subspecies of *Notropis cummingsae*

Fig. 1. *Notropis cummingsae cummingsae,* Carolina race: adult male, 34 mm. in standard length, from a tributary of South River, 1 mile south of Stedman, Cumberland County, North Carolina. Photograph by Art Smith.

Fig. 2. *Notropis cummingsae cummingsae,* Carolina race: adult female, 53 mm. long, from Nahunta Swamp, 1 mile north of Pikeville, Wayne County, North Carolina. Photograph by Douglass M. Payne.

Fig. 3. *Notropis cummingsae collis,* holotype: adult female, 34 mm. in standard length, from Roses Creek, Burke County, North Carolina. Photograph by Douglass M. Payne.

PLATE I

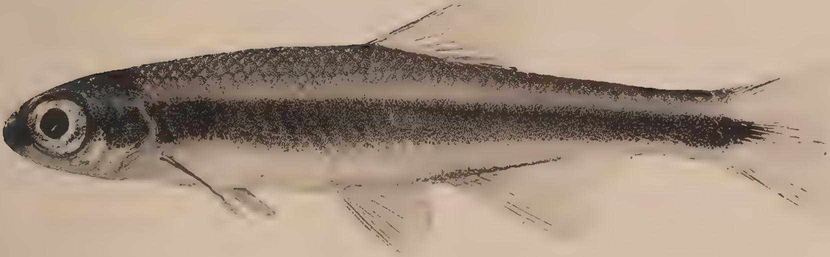

Fig. 1

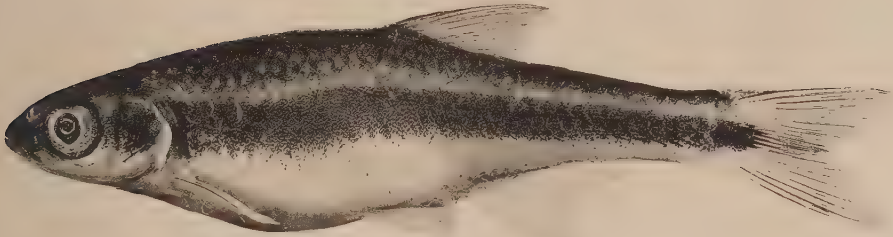

Fig. 2

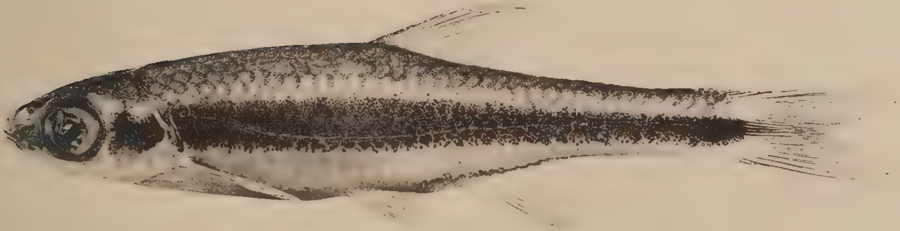

Fig. 3

The Effect of Winds and Tides on the Length of the Day

By YALE MINTZ[1] and WALTER MUNK[2], University of California

Abstract

The seasonal variation in the zonal winds of the atmosphere are reexamined and estimated to account for a January to July change of 0,5 milliseconds in the length of the day. Thus only one third of the change in length of the day reported by the astronomers is explained by angular momentum transfers between the earth and atmosphere. The corresponding effect of the varying equilibrium body tide of the earth caused by changes in the sun's distance and longitude is negligible.

ntroduction

Slight seasonal deviations of astronomic ime from accurate clock time have been eported by various astronomers, notably toyko, Finch and Uhink. If these variations re to be ascribed to seasonal variations in the arth's angular velocity, as has been suggested, hen the length of the day varies by two nilliseconds between early spring and late ummer and by 1.5 ms between mid-January nd mid-July. It is not yet quite certain whether his interpretation should account for all of he observed effect.

In a previous paper (MUNK and MILLER, 950) it was shown that ocean currents and hifts in air and water masses could play only a elatively minor role, whereas the seasonal ariations in zonal winds were estimated to ccount for a variation of 1.6 milliseconds in he length of the day. From new information on zonal winds (HUTCHINGS, 1950; MINTZ and DEAN, 1951) we now estimate this effect to be only one third as large. We have also computed the effect of seasonal variations in the earth's moment of inertia due to earth tides. This effect may account for some of the reported semi-annual component, but only a very small part of the annual component.

Astronomic observations

Measurements by Stoyko, Finch and Uhink give, on the average (STOYKO, 1951),

$$\Delta t = 58 \sin (\odot + 28^\circ) + 8.3 \sin 2 (\odot + 146^\circ),$$

for the difference in milliseconds between mean annual time and astronomic time, as function of the sun's longitude $\odot$. We shall assume this to be due entirely to variations in the earth's angular velocity. Differentiation yields

$$\Delta T_{\text{astr}} = \frac{2\pi}{365}\,\frac{d(\Delta t)}{d\odot} \doteq 1.00 \cos (\odot + 28^\circ) + 0.29 \cos 2 (\odot + 146^\circ)$$

for the anomaly in milliseconds in the length of the day.[1] The three observers differ on the average by 5 per cent with regard to the amplitude of the annual term, and by 24 per cent with regard to the semi-annual term. For the longest day, $\triangle T = 0.99$ ms, $\odot = 3°$ (March 24); for the shortest day, $\triangle T = -1.23$ ms, $\odot = 137°$ (Aug. 7).

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[1] U. C. L. A. Department of Meteorology, Papers in Meteorology, No. 12. The research reported in this aper has been sponsored in part by the Geophysical Research Division of the Air Force Cambridge Reearch Center under Contract No. 19 (122) —48.

[2] Contribution from the Scripps Institution of Oceanoraphy, New Series No. 543, supported under a contract with the office of Naval Research.

Earth tides

The fluctuation in the length of the day is due partly to seasonal changes in the semi-diurnal tides. There is a slight additional protuberance, on the average, in the equatorial region at the expense of the polar regions, and a resulting increment in the earth's moment of inertia by

$$\delta I = -k I \frac{M'}{M} \frac{r^3}{r'^3} (2-3 \cos^2 \Theta)$$

over what it would be if the sun were absent. Here $I = (1/3)\, Mr^2$ is the earth's moment of inertia, M its mass and r its radius; M', r' and Θ refer to the mass, the distance and the declination of the sun; $k = 0.27$ is Love's number. The essential effects here are variations $\triangle(\delta I)$ which occur because of seasonal changes in the heliocentric distance, by

$$\triangle r' = -0{,}0168\, r'_0 \sin(\odot + 168°),$$

and because of changes in the sun's longitude according to

$$\Theta = 23.5° \sin \odot$$

due to the obliquity of the ecliptic. The resulting variations in T, the length of the day, in ms, is

$$\triangle T_{\text{tides}} = \frac{\triangle(\delta I)}{I}\, T = 0.02 \cos(\odot + 73°) + $$
$$+ 0.15 \cos 2\odot .$$

Certain modifications may be required to allow for the difference in the yielding of land and sea to tidal forces.

The obliquity of the ecliptic, which leads to the semi-annual term in the above expression, can account for half the amplitude of the reported semi-annual effect, but not all, even if allowance is made for the large observational error. There is no agreement with regard to phase. Prof. JEFFREYS (1928) drew attention to this possible role of the obliquity on accurate time-keeping before this effect was discovered. A somewhat larger effect on $\triangle T$ must be expected from the variation in lunar tides, but because of the short period of this variation the effect on the cumulative time anomaly $\triangle t$ is relatively small and has not yet been observed.

Subtracting the tidal effect from the observed effect leaves

$$\triangle T_{\text{astr}} - \triangle T_{\text{tides}} = 0.98 \cos(\odot + 27°) + $$
$$+ 0.27 \cos 2(\odot + 131°)$$

to be accounted for by other causes. The difference mid-January minus mid-July equals 1.5 ms.

The effect of zonal winds

Because the total angular momentum of the earth and atmosphere are conserved, it follows that anomalies in the length of the day due to variations in zonal winds (MUNK and MILLER, 1950) are given by

$$\triangle T_{\text{wind}} = \frac{\triangle(I_a \omega_a)}{I \Omega_e}\, T,$$

where

$$I_a \omega_a = \frac{2\pi r^3}{g}\, p_0 \int_{-\pi/2}^{\pi/2} \tilde{u} \cos^2 \phi \, \delta \phi$$

is the angular momentum of the atmosphere, $I\Omega_e$ the angular momentum of the planet earth, g gravity, ϕ latitude, and where

$$\tilde{u} = \frac{1}{2\pi} \int_0^{2\pi} \delta\lambda \frac{1}{p_0} \int_{p_0}^{0} u \, \delta p$$

is the zonal wind averaged over all longitudes λ and pressures p.

In fig. 1, $(\tilde{u}_{\text{Jan}} - \tilde{u}_{\text{July}})$ is plotted against $\int_0^{\phi} \cos^2 \phi \, \delta \phi$. The area under the curve is therefore proportional to $(I_a\omega_a)_{\text{Jan}} - (I_a\omega_a)_{\text{July}}$.

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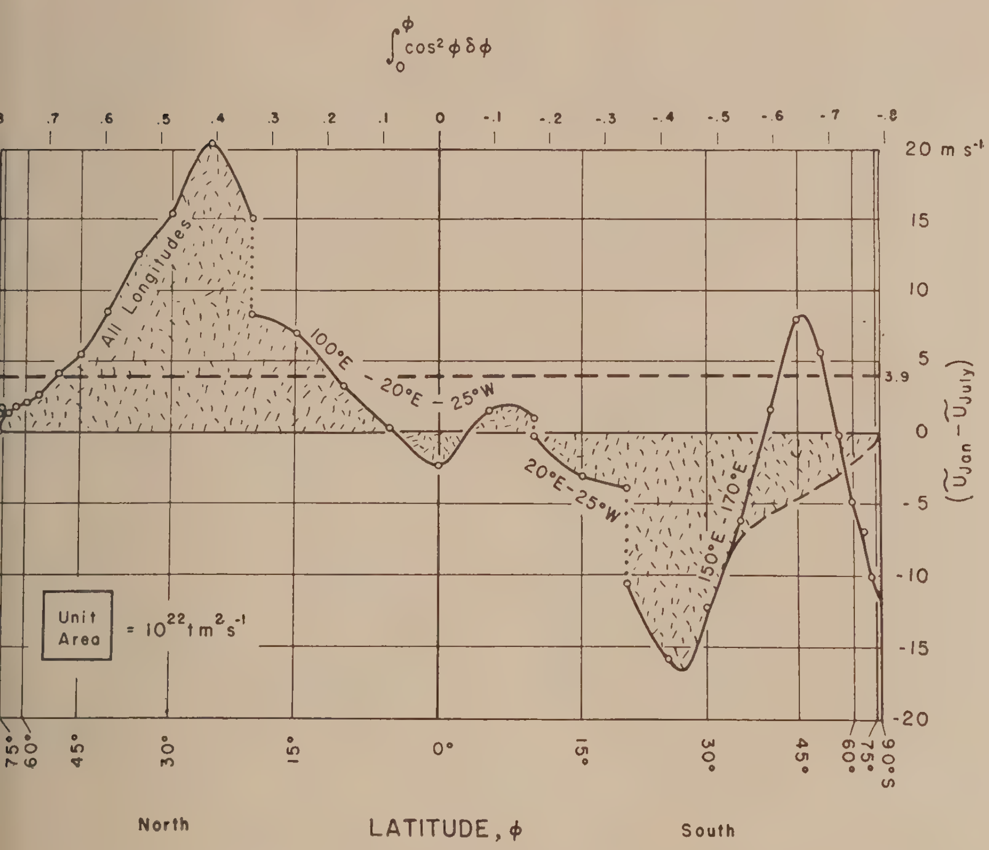
[1] Because of a numerical error STOYKO (1951) obtains only 0.17 ms for the amplitude of the semi-annual term.



g. 1. The seasonal change of zonal wind, as a function of latitude ϕ. The mean zonal wind $\tilde{u}$ is averaged from 1 to 0 cb and over all longitudes. The abscissa has been chosen as a particular function of ϕ for which the area der the curve is proportional to change in angular momentum: unit area equals 10^{22} t m^2 s^{-1}, corresponding 0.15 milliseconds in the length of the day. In order to account for a reported change of 1.5 ms, the mean value of the curve should equal 3.9 m s^{-1}, as indicated by the dashed line.

order to account for a difference of 1.5 ms, e mean value of ($\tilde{u}_{Jan}-\tilde{u}_{July}$) should equal 9 m sec⁻¹, as shown.

For the latitude belt 20°—90° North, ($\tilde{u}_{Jan}$— $_{ly}$) was computed from cross sections of the ean January and July geostrophic zonal winds eraged over *all* longitudes (MINTZ and DEAN, 51), between pressures 101 and 5 cb (instead sea level pressure p_0 and 0 cb), with the sults shown in fig. 1.

For the latitude belt 20°—75° South, ($\tilde{u}_{Jan}$— $_{ly}$) was computed from summer and winter oss sections of geostrophic zonal winds in e longitudes of New Zealand (HUTCHINGS, 50), from 101 to 5 cb; and east coast Australia (LOEWE and RADOK, 1950), from 101 to 15 cb, with the average for the two longitudes shown in the figure by the solid curve. The subtropical part of this curve was assumed to approximate conditions averaged over all longitudes of the southern hemisphere, [although this assumption is not without its uncertainties, as in the northern hemisphere the variation of ($\tilde{u}_{Jan}-\tilde{u}_{July}$) with longitude is as great as ($\tilde{u}_{Jan}-\tilde{u}_{July}$) itself; and in the southern hemisphere, at 30° S, ($\tilde{u}_{Jan}-\tilde{u}_{July}$) is 6 m sec⁻¹ greater at 170° E than at 150° E.] The temperate and higher latitude part of the solid curve shows the seasonal change of zonal wind in the region of the Ross Sea low (and upper air trough), and was not assumed to approximate conditions averaged over all longitudes. A plausible estimate of $(\tilde{u}_{Jan} - \tilde{u}_{July})$ averaged over all longitudes is given in the figure by the broken curve.

In the tropical latitudes $(\tilde{u}_{Jan} - \tilde{u}_{July})$ was computed from cross sections of summer and winter mean pilot balloon winds at longitudes 20° E and 25° W (Ekhart, 1941), from 101 to 30 cb; in addition, at latitudes 20° N to 10° S the January and July mean pilot balloon zonal winds at longitude 100° E, (Mintz and Dean, 1951), from 101 to 5 cb were used. The curves in the figure show the average results, with the longitudes indicated. It is uncertain how well these curves represent all longitudes. The tropospheric circulation in the tropics is divided into pronounced horizontal cells and there are large variations of zonal wind, and of seasonal change of zonal wind, with longitude. Moreover, pilot balloon observations are selective with respect to cloudiness and hence with respect to the zonal component of the wind. We note that the curves between 20° N and 20° S reveal only a small net effect. This result might be expected from the fact that at these latitudes the percentage of the earth's surface that is covered by land, the heights of the mountain barriers, and the seasonal change of the zonal wind at the ocean surface are about the same in the two hemispheres.

Table 1. Seasonal change of atmospheric angular momentum and the resulting changes in the length of the day, for stated latitude belts.

	90°N—20° N	20°N—20° S	20° S—90° S	90°N—90° S
$(I_a \omega_a)_{Jan} - (I_a \omega_a)_{July}$, in $10^{22} t$ m² s⁻¹	8.0	1.3	—5.9	3.4
$(\Delta T_{wind})_{Jan}$ — — $(\Delta T_{wind})_{July}$, in millisec	1.2	0.2	—0.9	0.5

By integration of the shaded area in the figure, the values in Table 1 were computed. According to these figures the winds account for only one third of the reported seasonal variation in the length of the day.[1] If the section along 150° E and 170° E in the souther hemisphere is used without adjustment (Fig. solid curve), the winds would account fo 0.8 ms, half the reported effect. Because of th large uncertainties in the calculations fo tropical and southern latitudes, our estimate may be greatly in error. It is not impossibl that instead of accounting for one third th reported effect the winds may account fo only a negligible part, or for more than ha of it. From an inspection of Figure 1 it doe not seem likely, however, that the winds ca account for all of the reported variation.

Thus in spite of the fact that our knowledg of the wind field is based on larger numbe of observations than are available for an other kind of geophysical quantity, the resul is uncertain, and will remain so for some tim to come.

No improvement is to be found by resortin to estimates of the surface zonal wind stre (van den Dungen, et al., 1950). A six mont change of 1.5 ms in the length of the da corresponds to an average rate of change c angular momentum of 0.7×10^{16} t m² s^{-2}. Bu the total westerly torque and the total easterl torque of the atmosphere on the earth ar each of the order of 10×10^{16} t m² s^{-2}, (Mint 1951). To come within 25 per cent of th seasonal change in length of the day, th surface torques would have to be compute to an accuracy of one part in one hundred!

Conclusions

Astronomic observations indicate that th mean length of the day in January exceed that in July by 1.5 milliseconds. It is howeve possible that this difference might be smalle due to periodic errors in the right ascensio system of the fundamental catalogue of sta places. More information on this point wi be available within the next few years, whe the new Greenwich Photographic Zenith Tub comes into action.[1] We may also expe increased accuracy from the improvement c clocks, possibly the use of atomic clocks.

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[1] Previous computations by Munk and Miller (1950) gave too high a value principally because in the northern hemisphere they used the published sections along 100 and 80° W, where, as it now turns out, the variations the zonal winds are larger than at all other longitude

[1] We are indebted to the Astronomer Royal for i formation concerning these developments.

Our present estimate is that the winds ount for 0.5 ms, but this estimate may be nsiderably in error due to uncertainties conning the tropical southern hemisphere winds. e circulation of the ocean, changes in sea el and shifts in air masses might possibly ntribute another 0.5 ms, but this is by no eans established (Munk and Miller, 1950). in each case we put down the largest possible mber, the combined effect might add up to 1.5 ms, but we do not suggest that this is the case.

One might hope to return to this problem when more complete meteorologic data are available, and to compute the effect for each month of the year. The principal needs are for station level pressure variations (not reduced to sea level), and for southern hemisphere upper air winds over the open sea

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SOCIETY OF ECONOMIC PALEONTOLOGISTS AND MINERALOGISTS
SPECIAL PUBLICATION NO. 2, PP. 53–65, FIGS. 1–8, NOVEMBER, 1951

TRANSPORTATION OF SAND INTO DEEP WATER[1]

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ABSTRACT

Well-sorted sand in deep water[2] has now been discovered in so many places that it can not be attributed to chance introduction. The nature of sand layers in between typical deep water deposits suggests rapid emplacement by some type of flow, presumably turbidity currents. The sand appears to be carried seaward along the axes of submarine canyons, the currents being generated by landslides at the heads of the submarine canyons. No evidence has been found to indicate that these flows are capable of cutting the rock gorges of the canyons. To date, artificial production of slides has been unsuccessful.

INTRODUCTION

As exploration of the sea floor has progressed, the geologic concept that sand and gravel are confined to shallow water environments has been shown to be unfounded. At first coarse sediment was discovered on the outer and deeper portions of the continental shelves. Then the exploration of submarine canyon axes and of the continental slopes indicated that sand and gravel were by no means confined to the shelves. Recently layers of well-sorted sand of all grades have been found in the basins, troughs, and even the deep trenches of the oceanic abyss.[3] If this coarse sediment were confined to areas where ice rafting had been an active cause of deep-sea sedimentation or if the coarse material had other indications of rafting, no modification of current opinions would be required. However, coarse material (fig. 1) has been found in many areas where ice rafting is most unlikely. Furthermore, deep-water cores contain sand layers which are far too well sorted for any chance introduction by rafting, and some of them show a gradation from coarse material underneath up into fine—a most unlikely arrangement if rafting were the cause. Introduction of the sand by wind is improbable because of the coarseness of some samples and because of the great distances involved.

The first reaction of some geologists, including the writer, to the occurrence of these coarse deep-water sediments was that they indicated large changes of sea level during the Pleistocene. Such an explanation, however, is made unlikely not only by the magnitude of the required changes, but by the finding of a succession of sand layers interbedded with typical deep-water sediments.

The submarine geology program at Scripps Institution has contributed to the explanation of the deep-water sands both directly and indirectly. Following the discovery of sand layers in San Diego Trough at depths of 3,000 feet, an intensive collection of cores was made in this trough to determine the sand distribution. These cores have been analyzed and studied by J. C. Ludwick (1950) and the foraminiferal content of many of them has been investigated by F. B. Phleger (this symposium, pp. 66–75). The repetition of sounding profiles in the

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[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 544. This work represents results of research carried out for the Office of Naval Research and Beach Erosion Board, Corps of Engineers, Department of the Army, under contract with the University of California.

[2] For convenience in this paper a deep water environment will mean one in excess of 250 fathoms (1,500 feet).

[3] Scattered reports of sand from the deep ocean date back to the Challenger Expedition, but these early discoveries were considered as rare exceptions.

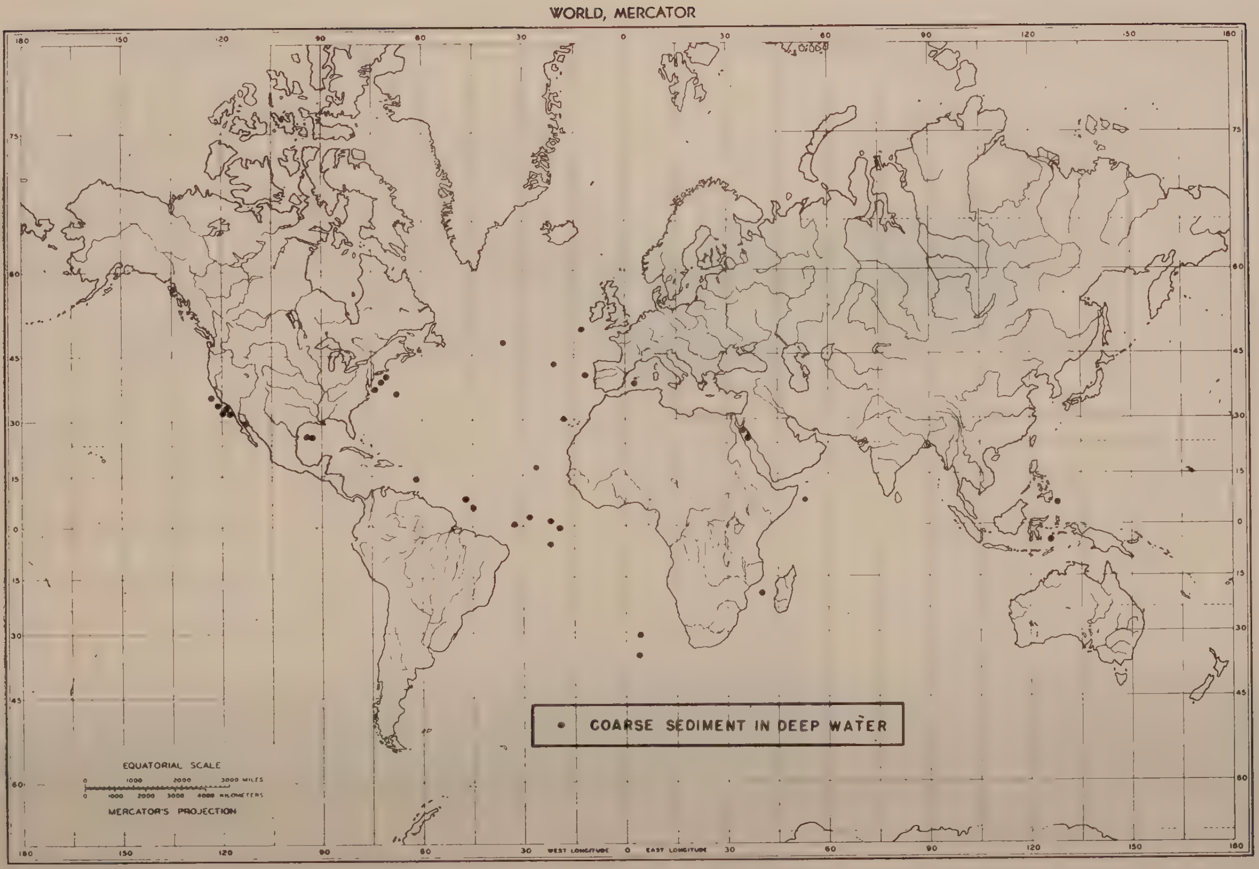
WORLD, MERCATOR
● COARSE SEDIMENT IN DEEP WATER
EQUATORIAL SCALE
0 1000 2000 3000 MILES
0 1000 2000 3000 4000 KILOMETERS
MERCATOR'S PROJECTION
WEST LONGITUDE
EAST LONGITUDE

FIG. 1.—Localities where cores have revealed the presence of sand layers in deep water. Cores containing probable ice-rafted material are omitted as are also all notations of coarse sediment from charts. Most of the information is derived from the Swedish Deep Sea Expedition, the cruises of the *Atlantis* and of the *E. W. Scripps*, and from the Piggot cores of the North Atlantic.

heads of La Jolla and Scripps submarine canyons has indicated that there are alternate periods of fill and deepening. Because the fill consists largely of sand and because the deepening presumably indicates that this sand is discharged down the canyon axes, a means of introduction of sand into deep water is indicated. As a result a considerable collection of cores was made along the axis of La Jolla Canyon. Attempts were made also to investigate the nature of the sand movements by setting off explosions along the canyon axis.

ACKNOWLEDGMENTS

The results reported in this paper are to a considerable extent a compilation of recent submarine geologic exploration and include reference to deep-water cores kindly supplied to the writer by Doctors Hans Pettersson, Maurice Ewing, and K. O. Emery. Extensive use has been made also of cores obtained by Scripps Institution over a period of many years. Most of these were analyzed under the direction of Dr. Roger Revelle. Much information comes from studies of cores made by J. C. Ludwick. The Navy Electronics Laboratory vessel USS EPCE(R)-857 was made available for some of the work in cooperation with Dr. R. S. Dietz of that laboratory. Important information was supplied by Dr. Fred B. Phleger. Field and laboratory assistance was provided by J. D. Frautschy, D. L. Inman, D. B. Sayner, Ruth Young, Robert Norris, and G. E. Brayton. Great appreciation is expressed for all of this active coöperation.

WORLD-WIDE DISTRIBUTION OF DEEP-WATER COARSE MATERIAL

Figure 1 indicates roughly the widespread occurrence of deep-water sand layers. In some localities a considerable number of finds are indicated by only one dot because of the small scale. The map gives the impression that there are few localities with deep-water sands, but actually sand has been reported from a large per cent of the total deep-water cores from which information is available. Hans Pettersson's oral reports from his world cruise on the *Albatross* and Maurice Ewing's reports from his Atlantic cruises on the *Atlantis*, indicate that there are many other localities with sand in the deep ocean.

Most of the sand layers from the oceanic abysses were found at or near the base of the continental slopes, or in trenches bordered by appreciable slopes. However, the slopes adjacent to many of the deep sand localities are gentle, that is, of the order of 1° to 5°, and in some cases the sand layers occur many miles out beyond the slope bases. Examples of sand transport over gentle or negligible slopes include:

1. Thick sand layers covered by globigerina ooze obtained by the Swedish Deep Sea Expedition from the deep Atlantic 600 miles northeast of the mouth of the Amazon River.[1]
2. Sand layers from the flat portion of the Sigsbee Deep in the Gulf of Mexico (Trask et al., 1947); 200 miles off the Rio Grande and 140 miles from the edge of the continental shelf.
3. The thin sand layers reported first by H. C. Stetson and later by Maurice Ewing from the flat portions of the Bermuda Deep, hundreds of miles from the nearest appreciable slope.

According to present indications, however, sand is absent in most other cores from the deep, flat portions of the ocean floor.

Sand and gravel have been reported from numerous localities by surveyors from the deep portions of the continental slopes but, because of the uncertainty of the nature of these coarse sediments, they were not included in figure 1. A compilation of bottom notations on hydrographic charts from the slopes of the world (made by the writer) showed that sand constitutes about 25 per cent of the total and that rock and gravel (which were not differentiated) contribute another 10 per cent. The coarse sediment proved to be somewhat more abundant on the upper

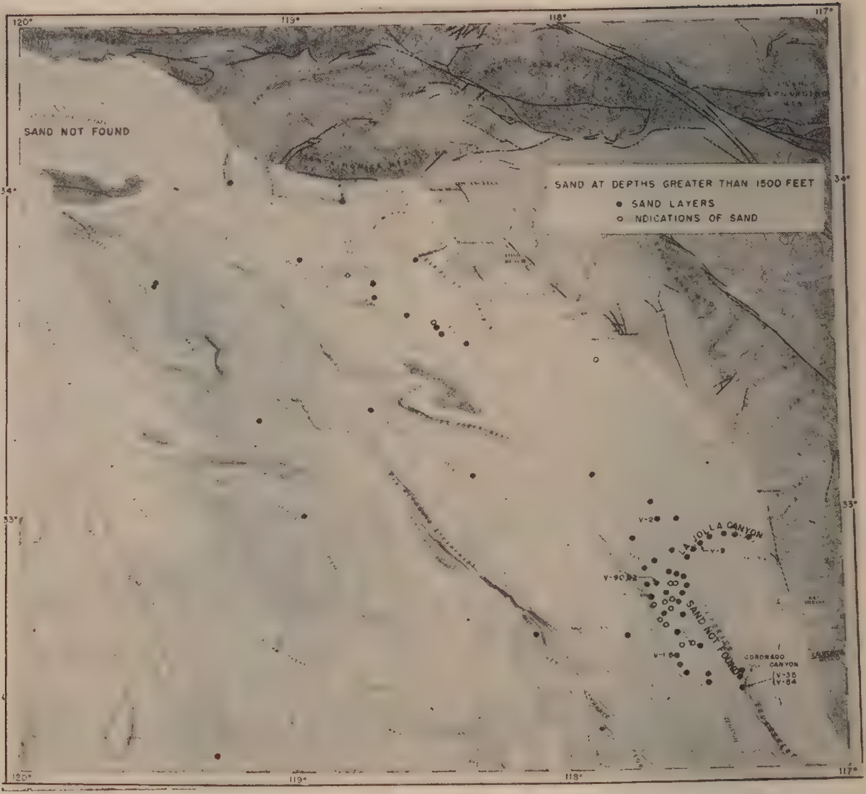
120°
119°
118°
117°
SAND NOT FOUND
34°
33°
SAND AT DEPTHS GREATER THAN 1500 FEET
● SAND LAYERS
○ INDICATIONS OF SAND
V-2
LA JOLLA CANYON
V-8
V-90
SAND NOT FOUND
V-1
CORONADO CANYON
V-35
V-84

FIG. 2.—Localities where cores have yielded sand layers or indications of sand off southern California. The relative abundance of dots is due in part to the abundance of coring localities. Note that two localities have indications that sand is not present. The "V" station numbers refer to cores containing significant Foraminifera cited by Phleger in this symposium

slopes but was by no means rare at depths in excess of 1,000 fathoms.

SAND LAYERS FROM TROUGHS AND BASINS OFF CALIFORNIA

Topographic Relations

The coring operations of the Scripps Institution, augmented by recent work by the Allan Hancock Foundation of the University of Southern California and the U. S. Navy Electronics Laboratory, have shown that sand is a common type of sediment in the deep basins and troughs of the continental borderland off the southern California coast (fig. 2). At present far too little is known of the details of the distribution of this sand over most of the borderland, although our extensive coring operations in San Diego Trough provide an exception. Available data indicate that sand layers off California occur at depths up to at least 1,000 fathoms and at distances of at least 120 nautical miles from the mainland. The outermost sand (not shown on fig. 2), found by K. O. Emery, is from a deep basin surrounded by ridges which are all deeper than 400 fathoms.

Some of the sand layers discovered by Emery in the inner basin contain char-

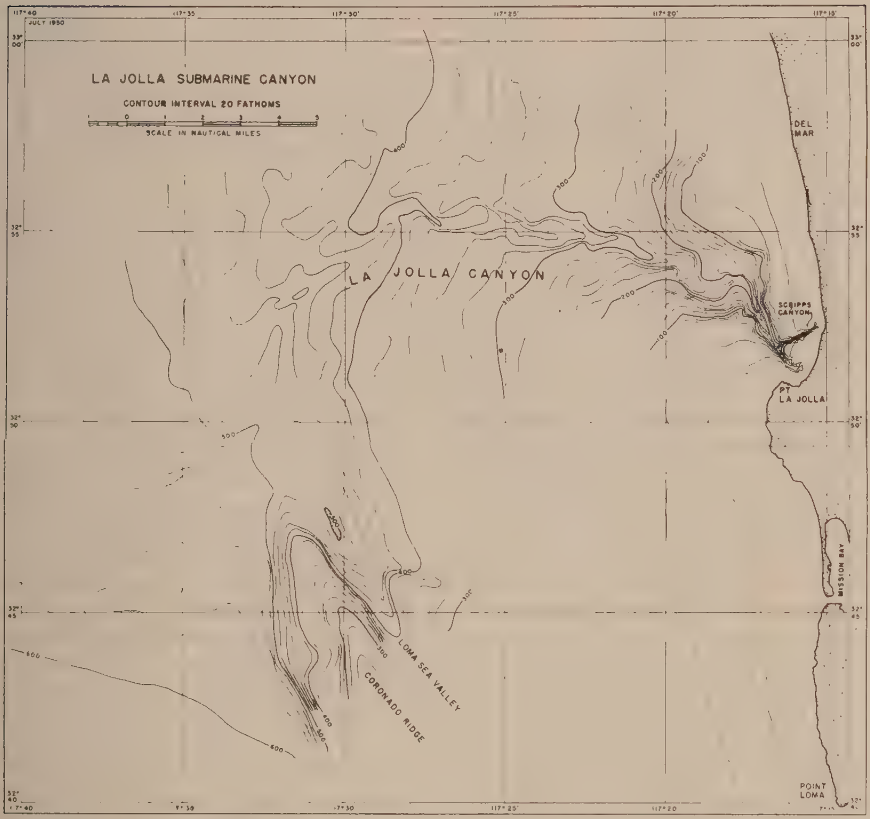
JULY 1950
LA JOLLA SUBMARINE CANYON
CONTOUR INTERVAL 20 FATHOMS
SCALE IN NAUTICAL MILES
117°40
117°35
117°30'
117°25'
117°20'
117°15'
33° 00'
32° 55
32° 50
32° 45
32° 40
DEL MAR
LA JOLLA CANYON
SCRIPPS CANYON
PT LA JOLLA
MISSION BAY
LOMA SEA VALLEY
CORONADO RIDGE
POINT LOMA
100
200
300
400
500
600

FIG. 3.—La Jolla submarine canyon. The presence of an outer valley approximately 20 fathoms deep is clearly indicated out to depths of 540 fathoms, but there is considerable uncertainty as to its continuation at greater depths. Based on recent surveys from U. S. Navy Electronics Laboratory and Scripps Institution vessels with some utilization of older Coast & Geodetic Survey soundings.

coal which he thinks implies derivation from the erosion of areas where forest fires had occurred.

The distribution of sand in the inner basins appears to be somewhat haphazard but may have some relationship to the submarine topography. Ludwick (1950) has shown that in San Diego Trough the sand is most abundant off the outer portion of La Jolla Submarine Canyon (figs. 2 and 3), whereas it is entirely lacking in the cores from the base of the slope off the relatively straight west side of Coronado Bank. Along the west side of the trough, adjacent to Thirty Mile Bank, a hard-packed sand has been encountered which is difficult to core.

To the north, San Pedro and Santa Monica Basins have sand which appears to be more common on the west side of the basins than on the east. Santa Barbara Basin has not yielded any sand layers to date. It is perhaps significant that the runoff into this basin is somewhat larger than into the basins to the south, thus providing more mud sediment.[4] Furthermore, Santa Barbara Basin differs from most of the others in that its sides lack any appreciable submarine canyons, the significance of which is explained later.

Nature of the Sand

So far as is known, the sand occurs in distinct layers, although in a number of cases very short cores provided only sand, indicating either that the sand was too thick or too hard-packed to allow the penetration of the coring device into the underlying material. All long cores contain a predominance of mud, that is, homogeneous material of silt and clay size. The sand appears to have a sharp lower boundary and in some cases a sharp upper boundary. Sand is found at the top of some of the cores. In other cases the sand grades into the overlying mud. One core obtained by R. S. Dietz showed alternate beds of silt and sand. The large number of samples analyzed by Ludwick provide substantial data concerning the nature of the sand from San Diego Trough. The grain size is confined largely to fine sand (Wentworth scale) and it is not as variable as is the sand found in the tributary submarine canyons. Several layers of sandy appearance were proved by analysis to be coarse silts.

The sorting of the sand (and the coarse silt) is exceptionally good. According to Ludwick, the median of the Trask sorting coefficients is 1.36, which is distinctly better than sorting in most continental shelf sands and approaches that of beach sand. Good sorting is particularly significant because the sands are found in an environment where, unless deposition is very fast, one would expect silt and clay to be contributed as the result of flood waters sweeping out over the sea as suspension clouds of low salinity (Bell, 1942) or as the product of offshore wind transport during the "Santa Ana" (northeast) blows.

A casual inspection of the sand layers from San Diego Trough fails to reveal any appreciable vertical grading from coarse to fine. However, Ludwick found by close inspection under binoculars that many of the layers do actually have such a gradation. It is probable that a routine field examination of rock layers formed from sediments of this type would not indicate gradation. The layers in the cores are often bent or discontinuous which may represent distortion in coring, but probably indicates slumping or other type of deformation on the bottom.

SAND SLUMPS IN SUBMARINE CANYON HEADS

Measurement of profiles along ranges in the nearshore heads of California submarine canyons was begun in 1933. Since that time the repetition of these profiles has indicated that depth changes are relatively frequent. Extremely precise methods have been developed in the work at La Jolla. A series of profiles are repeated in Scripps and La Jolla Canyons several times a year. To date there have been few changes in La Jolla Canyon, but the tributaries at the head of Scripps Canyon are constantly being filled and reopened (fig. 4). The fill consists largely of sand, but a great abundance of eel grass and kelp is deposited in the canyon and accumulates along with the sand. This marine vegetation decays and becomes a soft, stinking mass of slimy material. During the course of diving operations in these canyon heads the diver observed an abundance of these plants (Shepard, 1949). There is so much marine vegetation deposited in the canyons that its decay sets up continuous streams of methane gas bubbles which are invariably encountered at the surface over portions of the canyon head. The diver obtained photographs of these bubbles emerging from the sandy floor. This gas must decrease the cohesion of the sand. One can scarcely doubt that the water and gas pockets associated with kelp and eel grass are helpful in

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[4] The runoff would also contribute more sand, but only the fines are carried out in the low salinity surface flows which accompany heavy runoff.

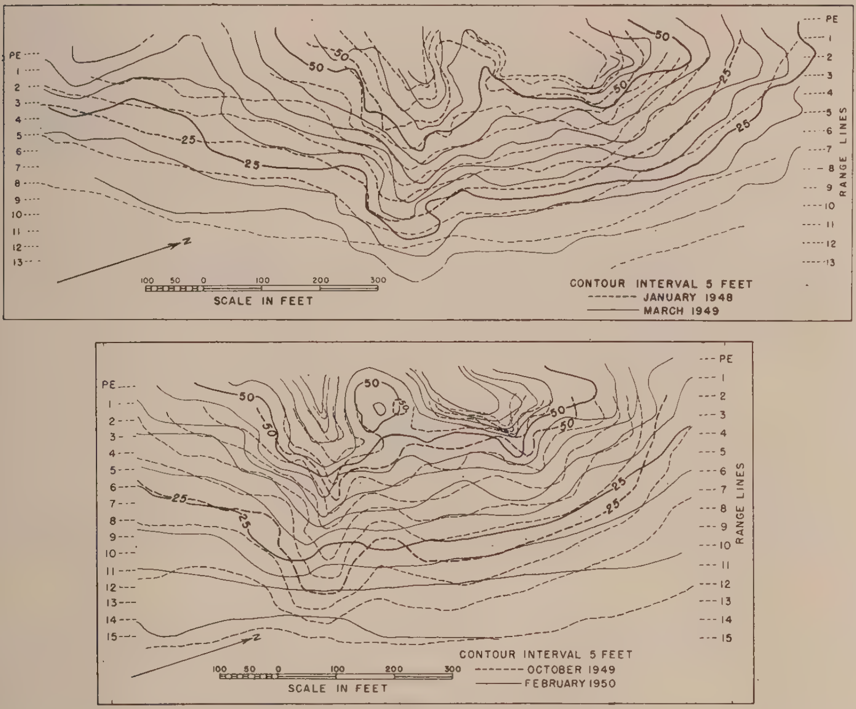
PE
1
2
3
4
5
6
7
8
9
10
11
12
13
RANGE LINES
50
25
Z
100 50 0 100 200 300
SCALE IN FEET
CONTOUR INTERVAL 5 FEET
JANUARY 1948
MARCH 1949
PE
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
RANGE LINES
50
25
Z
100 50 0 100 200 300
SCALE IN FEET
CONTOUR INTERVAL 5 FEET
OCTOBER 1949
FEBRUARY 1950

FIG. 4.—A cycle of cut and fill in the nearshore heads of two tributaries to Scripps Canyon. Based on frequent repetition of sounding lines along the indicated ranges.

setting off slides in the sand which is accumulating on these steep inclines.

Analyses of the sediment in these branches of Scripps Canyon, where slides occur, show that the material consists of fine- to medium-grained sand with a small amount of silt. Therefore, we have a possible source of sand, at least for the area in the vicinity of the mouth of La Jolla Canyon (Scripps Canyon is tributary to La Jolla). It has been estimated that the slides from Scripps Canyon head displace more than one million cubic feet of sand every year.

Ocean piers built into the heads of submarine canyons along the California coast have provided evidence of these slides. At Redondo one deepening of 25 feet took place over a period estimated by fishermen as about one half hour and was accompanied by swirls of sediment coming up into the surface water. These slides are reported both during stormy periods and during relatively quiet wave conditions. There is some evidence indicating that a slide occurred at La Jolla as the result of a small earthquake (fig. 5).

Uncertainty exists regarding the mode of transporting the sand out into the deep trough along the decreasing slope of the canyon floor (fig. 3). It does not seem entirely likely that a slide of material of sand size could continue down a gradient which becomes reduced to as low as about one per cent in the outer portion. However, the sand may be thrown into a turbidity current which, judging from experiments by Kuenen (1950, pp. 101–109), might continue at these low gradients and, in fact, might flow for some distance

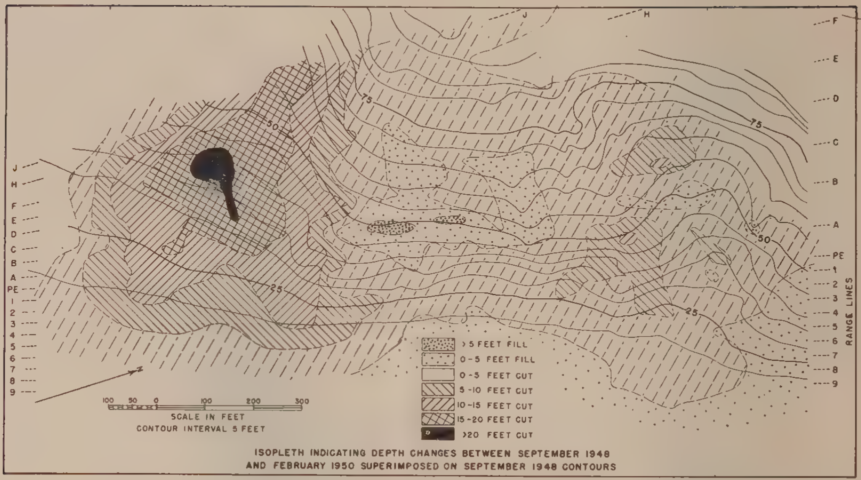
J
H
F
E
D
C
B
A
PE
1
2
3
4
5
6
7
8
9
RANGE LINES
75
50
25
100 50 0 100 200 300
SCALE IN FEET
CONTOUR INTERVAL 5 FEET
>5 FEET FILL
0-5 FEET FILL
0-5 FEET CUT
5-10 FEET CUT
10-15 FEET CUT
15-20 FEET CUT
>20 FEET CUT
ISOPLETH INDICATING DEPTH CHANGES BETWEEN SEPTEMBER 1948
AND FEBRUARY 1950 SUPERIMPOSED ON SEPTEMBER 1948 CONTOURS

FIG. 5.—Differences of depth (indicated by shading) which occurred in an area just to the south of that represented by figure 4. A larger change was observed along one line after a small earthquake in October, 1949, but most of the lines on which the entire change is based had not been surveyed since 1948.

over a horizontal floor.

CANYON FLOOR EXPLOSION TESTS

A group from the U. S. Navy Electronics Laboratory under R. S. Dietz joined with a Scripps Institution party in attempting to develop sand slides or turbidity currents in Scripps Canyon by setting off explosives on the canyon floor (fig. 6). The *E. W. Scripps* was anchored over the canyon axis downstream from the localities where the explosions were detonated and search was made for the movement of turbid water down the canyon, through the use of a turbidity meter consisting of a light source and a photoelectric cell mounted about 30 cm apart on a tripod and set near the bottom. The turbidity meter was connected with a microammeter placed on deck. During a second series of explosions current meters, sediment traps, and water samplers were used in addition to the turbidity meter.

To date the results of the explosions have proved disappointing and largely negative aside from some records obtained from the turbidity meter. When the explosions were set off in shallow water a large mass of turbid water boiled up to the surface, along with decaying eel grass and numerous fish. In no case did the turbid water from the shallow explosions reach the *E. W. Scripps* anchored at distances of 1,000 to 2,000 feet down canyon. However, explosions set off at distances of 130 to 700 feet produced a flow of turbid water past the tripod on the canyon floor. The arrival times indicate that the flow was moving from 20 to 36 cm per second, one flow being as fast as 60 cm per second. These velocities are scarcely greater than normal canyon floor currents which, if flowing in the down canyon direction, would transport the sediment stirred up by the explosion to the vicinity of the turbidity meter. The faster flows, however, suggest that the density of the water induced a slight current. The turbid flow had variable thickness (found by raising the tripod), mostly less than about 25 feet. A small amount of sand was obtained, presumably from the flows. Depth

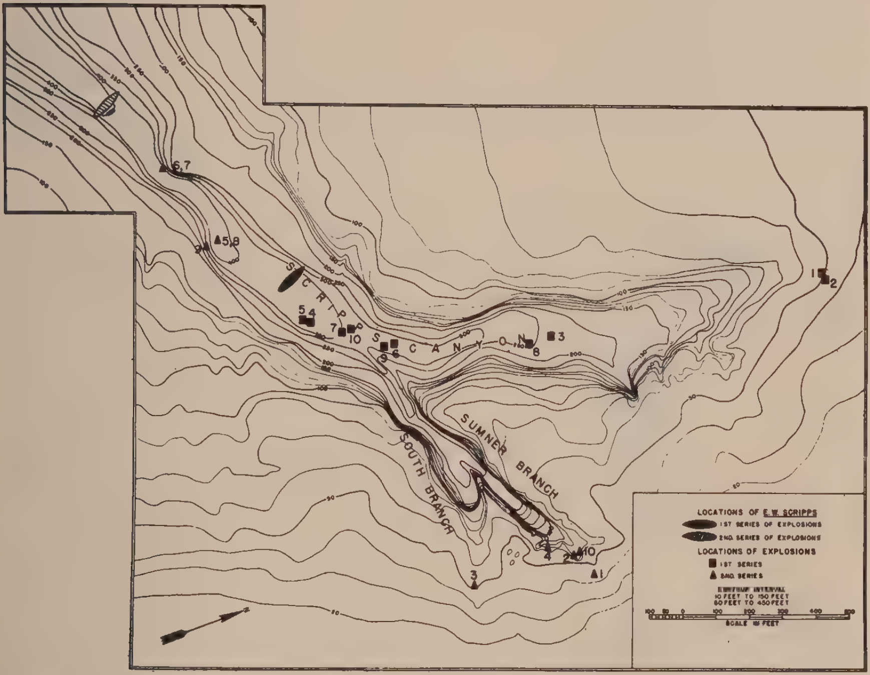
SCRIPPS CANYON
SUMNER BRANCH
SOUTH BRANCH
6,7
5,8
9
5 4
7
10
6
8
3
1
2
4
10
3
1
LOCATIONS OF E. W. SCRIPPS
1ST SERIES OF EXPLOSIONS
2ND. SERIES OF EXPLOSIONS
LOCATIONS OF EXPLOSIONS
1ST SERIES
2ND. SERIES
CONTOUR INTERVAL
10 FEET TO 150 FEET
50 FEET TO 450 FEET
100 50 0 100 200 300 400 500
SCALE IN FEET

FIG. 6.—Locations of the explosives set off on the canyon floor in an attempt to produce slides or turbidity currents. The location of the *E. W. Scripps*, from which instruments were suspended, is indicated for the two occasions.

changes accompanying the explosions were not greater than 2 or 3 feet and so far as known were confined to the immediate vicinity of the explosion.

The short distance of observed turbid flows shows that moderate amounts of mud and sand set into suspension by explosions do not develop turbidity currents which are self-perpetuating in moving down the canyon axes. As slopes at the canyon head are as great as 10° or more, this failure cannot be ascribed to low slopes. It appears that explosions alone are not enough to set off appreciable sand slumps on the canyon floor. However, they might act as a trigger effect if conditions had reached a degree of instability which required only a shock to produce movement. Further attempts should be made to set off one of the slides during a period of maximum fill. This was not possible in the first tests. Burying of the charges in the sediment may also have different effects from setting them off on the bottom, although the heavy mass of water overlying the surface charges drives considerable force into the bottom.

SAND LAYERS IN SUBMARINE CANYONS

The discovery of frequent sand slumps in submarine canyon heads and of a concentration of sand outside La Jolla Canyon in San Diego Trough, led to a careful exploration of the sediment along the axis of La Jolla Canyon (fig. 3). The results of this exploration apparently provide the necessary link between the sands of the canyon heads and those of the trough. Virtually every canyon core either had

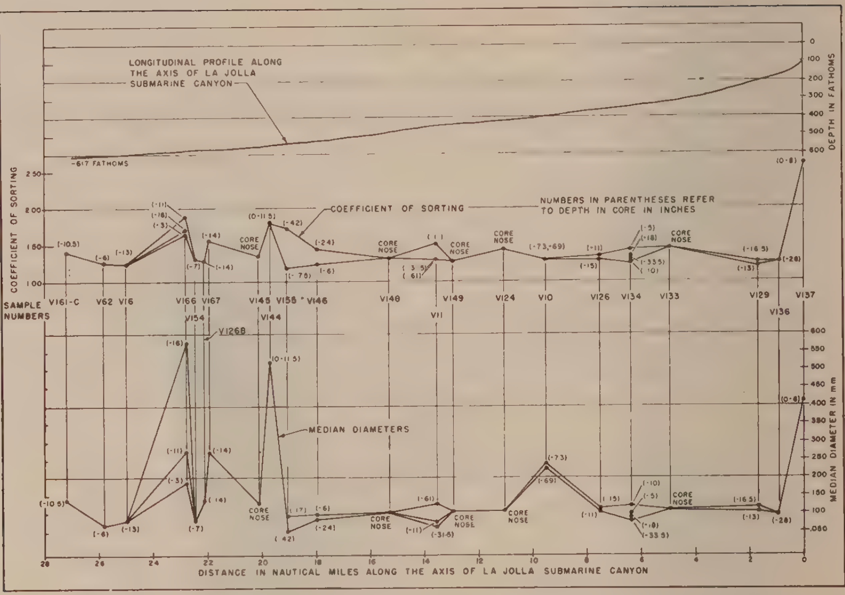

FIG. 7.—The variation of the sand layer characteristics along the axis of La Jolla Canyon (after Ludwick, 1950). Note that the lower portion of the canyon profile is beyond the terminus indicated in figure 3 and refers to the slope in San Diego Trough.

sand layers or sand grains adhering to an empty core barrel indicating penetration into sand. Figure 7, taken from Ludwick's analyses, indicates that the great bulk of the sand is fine-grained, having a median diameter between 0.05 and 0.25 mm. Diameters of this same size are most common in the fill near the canyon head inside the portion investigated by Ludwick. Medium- and coarse-grained sands were found near the canyon mouth at depths of 550 to 600 fathoms. Coarse sand was also discovered at a depth of 100 fathoms. The coarse material, both in shallow and deep water, is out of accord with the other sediments along the canyon, but it could have been derived from the sandstones of La Jolla Head where coarse sand beaches are found. The sand from 100 fathoms contained small clay pellets comparable to the clay lumps sometimes found in sandstones with slump structures.

The sand layers from La Jolla Canyon resemble those from San Diego Trough in the high degree of sorting. The median of the Trask sorting coefficients is 1.3. The sorting is somewhat better in the fine sands than in the coarse, as is commonly the case (Inman, 1949). According to Ludwick, the muddy sediments between sand layers differ from those in the San Diego Trough in having coarser medians with higher silt to clay ratios. In some of the shoaler samples the mud is definitely a coarse silt with little if any clay.

Numerous other cores have been taken from submarine canyons both on the east and west coasts. Sand is a common constituent of these cores, and gravel is by no means rare. Thus Maurice Ewing (personal communication) reports gravel from the bottom of a core in the outer portion of Hudson Submarine Canyon at depths in excess of 2,000 fathoms. The sediments obtained from east coast canyons have many zones where the medians are of sand size or very coarse silt (Stetson, 1949). Other sand layers may have been overlooked because of the method of composite analysis of 3 to 4 inch sections of the core. Coring, dredging, and snapper sampling have yielded sand from most of the canyons off the California coast (Shepard and Emery, 1941). In Monterey Canyon a 16-inch core from a depth of 840 fathoms showed a gradation from silt and clay at the surface down into gravel $2\frac{1}{2}$ inches in diameter at the bottom (fig. 8). The analysis shows one zone where only sand was reported below a layer with gravel. However, it is possible that the gravel was extracted or lost from this sand zone during field operations. An almost perfect gradation from silt to gravel is described by Inman (1950) from Mugu Canyon. Ludwick (1950) describes a gradation from a coarse shell sand and gravel up into silt from Coronado Canyon at 640 fathoms.

The earlier suggestion by the writer that the coarse sediment represents an uncovered remnant of deposition during a formerly elevated state of the canyons can now be ruled out, because normal deep-water deposits have been found beneath the sand layers and under one of the gravel layers.

TRANSPORTATION OF THE DEEP-WATER SANDS

Our present information concerning the deep-water sand layers indicates that sand and even gravel can be transported out into deep water. The studies of Foraminifera in deep-water cores reported by Phleger (this symposium, pp. 66–75) provide ample additional proof of this statement. The deep-water origin of some of the coarse Pliocene sediment of the Los Angeles and Ventura regions proposed by Natland (this symposium, pp. 76–107) and the result of his painstaking field and laboratory studies are definitely supported by the marine studies off southern California. The Pliocene formations have a greater amount of gravel than is found in the present day deep-sea troughs, but this can be explained by the absence of gravel formations along the slopes leading down into the present day troughs, whereas gravel deltas may have been building forward into the Pliocene troughs or into the heads of Pliocene submarine canyons, if such existed.

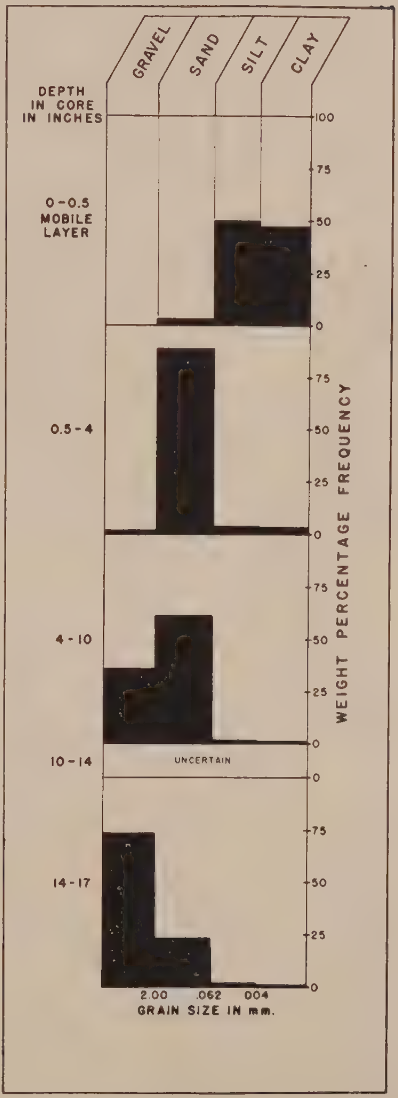

FIG. 8.—Graded bedding in a 17-inch core obtained from the axis of Monterey Canyon in 835 fathoms. Histograms indicate the variation in sediment at various depths in the core.

The nature of the sand and gravel movements into deep water remains somewhat of a mystery. The tank experiments performed by Kuenen indicate that turbidity currents may be the explanation, although some of the deep-sea formations described by Natland have the appearance of mud flows or other type of submarine slumping rather than of turbidity current deposits such as Kuenen produced in the laboratory. As yet we have no good evidence of the nature of movement which occurs when a canyon fill is removed. The material may start moving as a sliding mass which is thrown into turbulent aqueous transport as it proceeds down the canyon axis. It is easier to understand the continuation of movement out over the relatively horizontal floors of basins and troughs as a turbidity current than as mass transport in a mud flow or a sand slide.

POSSIBLE CANYON EROSION BY SAND TRANSPORT

The effect of the transport of sand along the canyon floors on canyon formation remains to be determined. It is as possible for a rapidly flowing turbidity current charged with sand and gravel to erode a canyon floor as it is for a stream, but as yet we do not have any evidence that the mud and sand can form a turbid layer of sufficient density to produce such a fast flow. The canyon cores which penetrate through sand layers into underlying mud layers suggest that the flows responsible for these sands were unable to erode the soft mud underneath. Kuenen and Migliorini (1950, pl. 5A) show other instances where coarse sediment was moved over mud surfaces without even destroying worm tracks in the mud.

The flat floors of the canyons, which exist even after the periodic deepenings, suggest that the fill is not normally removed from the canyons during flows. The discovery of cold water Foraminifera in the mud under the post-glacial fill of the Georges Bank Canyons (Phleger, 1939), indicates that during the thousands of years following the deposition of the glacial stage fill any flows taking place in those canyons must have been inconsequential and certainly not of erosive character. It may be that greatly elongated cores obtained by the new Kullenberg instrument will prove that deposition has been proceeding in the east coast canyon axes through a large part of the glacial period. Should this be the case, the hypothesis that submarine erosion has caused the canyons during glacial stages would have to be abandoned.

TANK TURBIDITY CURRENT DEPOSITS COMPARED TO DEEP-WATER SANDS

Graded bedding, poor sorting, wide continuity of beds, and lack of cross-bedding have been postulated by Kuenen and Migliorini (1950, p. 92) as possible criteria for the recognition of ancient turbidity current deposits. If, however, the sand beds from the recent deep marine sediments were transported by turbidity currents, these criteria, based mostly on tank studies, may not have much significance. The sand beds in deep-water cores are almost invariably well-sorted, grading is ordinarily quite inconspicuous, and the sand layers are, so far as known, not continuous (Ludwick, 1950). On the other hand, only one deep-sea core shows signs of cross-bedding (Trask et al., 1947) and graded bedding is clearly shown in some of the cores from submarine canyons. A further suggestion that graded bedding is not necessarily a characteristic of the coarse sediments of deep water was provided by a recent opportunity to visit Manley Natland's classical locality, in the Ventura, California, area, where the Foraminifera provide good evidence of deep-water deposition. At these localities many layers of sandstones interbedded between mudstones showed no apparent grading. Elsewhere, however, graded beds of sand were seen along with gradations from conglomerate up into sandstone and in some cases into mudstone.

SUMMARY AND CONCLUSIONS

At the present stage of marine investigations the conclusion seems warranted that sand sediments are almost commonplace in deep water environments at or near the base of slopes. As some of these coarse sediments occur at or near the top of the cores and because they are commonly interbedded with clays and oozes typical of deep-water conditions, it is probable that sands are still being introduced. Most of the sands studied are well-sorted. Some of them show graded bedding, but this is not ordinarily a conspicuous characteristic. In San Diego Trough, where the sand has been cored in numerous localities, the discontinuous nature of the layers is indicated. The sands of this trough are most abundant off the mouth of a submarine canyon. Cores from the axis of the same canyon have many sand layers. Furthermore, sand is being deposited in the canyon head and this deposition is often interrupted by submarine slides.

The evidence found in San Diego Trough and La Jolla Canyon suggests that, at least in this area, the sand probably is carried to its present deep-water environment by a combination of slumping and turbidity currents. The suggestion is made that slumps, such as are known to occur in the shallow coastal water at the heads of submarine canyons, are converted into turbidity currents of the type shown in Kuenen's experiments and that these currents carry some of the coarse sediment out along the axes of canyons, depositing it on the floors of troughs and basins beyond. It is not unlikely that slumps take place also on submarine slopes well out from the land, although the chance of acquiring a large supply of sand for transportation down the outer slopes is not as good as it is at the near-shore canyon heads where rapid sand deposition takes place. It is suggested also that the accumulation of decaying kelp and eel grass in canyon heads has an important effect in permitting the sand slides to occur. It is possible that the sand layers found on the deep sea floor off the east coast, where the canyon heads are many miles from shore, were the result of slides initiated during glacial stages. At such times sand and masses of marine vegetation could have been supplied to the canyon heads just as they are now supplied to many of the canyons off the California coast.

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DISPLACED FORAMINIFERA FAUNAS

BY

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Reprinted from
Society of Economic Paleontologists and Mineralogists
Special Publication No. 2, pp. 66-75, November, 1951

Society of Economic Paleontologists and Mineralogists
Special Publication No. 2, pp. 66–75, Figs. 1–7, November, 1951

DISPLACED FORAMINIFERA FAUNAS[1]

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ABSTRACT

Deep-sea sands from the San Diego Trough and the Sigsbee Deep contain shallow-water species of Foraminifera and appear to have been displaced by turbidity currents. The faunas suggest different types of movement for some of the sands in which they occur.

INTRODUCTION

Numerous local sands have been discovered in deep marine areas where only mud might have been expected. It is now presumed that most or all of these sands were originally deposited in relatively shallow water and have been displaced by movement of sediment down slope. Recent studies show that some deep-water sands contain benthonic Foraminifera characteristic of much shoaler water than the depths at which they were collected. The purpose of this paper is to give the present faunal evidence for displacement of some of these sands from relatively shoal into deeper water in the San Diego Trough, off San Diego, Calif., and in the Sigsbee Deep in the western Gulf of Mexico. This is a preliminary report and the results are subject to further verification or modification.

Tests of Foraminifera may be considered an integral part of the sediment in which they occur. They behave as mineral grains, at least after the death or reproduction of the animal, and will be transported and modified along with the enclosing sediment. The specimens lived in a community conditioned by complex environmental factors and record the details of the environment in which they lived. Thus they are useful tools in discovering anomalies of distribution of the sediment in which they occur.

The evidence for downslope movement of Foraminifera faunas is based upon what is known of depth ranges of Foraminifera in each area being considered. Depth ranges are fairly well established for the western Gulf of Mexico. Less is known about depth biofacies of Foraminifera in the San Diego region, but sufficient work has been done to obtain a general picture of some of the distributions.

ACKNOWLEDGEMENTS

Sediment samples from the San Diego Trough were collected for the writer by J. D. Frautschy using the *E. W. Scripps*, research vessel of the Scripps Institution of Oceanography. Core samples were furnished by J. C. Ludwick and F. P. Shepard. The two cores from the Gulf of Mexico were collected by C. R. Hayes, using the research vessel *Atlantis* of the Woods Hole Oceanographic Institution. Frances L. Parker has done much of the laboratory work on depth ranges of Foraminifera in the San Diego area, and Jean F. Peirson has drawn the illustrations. This work was financed by the Office of Naval Research as Project No. NR 081 050.

BENTHONIC POPULATIONS OFF SAN DIEGO

There is little usable information on the ecology of Foraminifera off the coast of southern California. One notable exception is the work of Natland (1933) on samples taken between San Pedro and Santa Catalina Island. Samples have been collected from the eastern side of the San Diego Trough extending from the upper part of the continental shelf to the average depth of the floor of the trough at this place. These samples are grouped into four traverses, and were taken from approximately 100 stations. The sediment was collected with a small snapper sampler in sand areas, and a short coring tube was used in mud and mud-sand areas. The samples came from depths ranging from approximately 10 fathoms to 650 fathoms.

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[1] Contributions from the Scripps Institution of Oceanography, New Series, no. 545, Contribution no. 6, Marine Foraminfera Laboratory.

DEPTH RANGES OF SPECIES

Insufficient data have been collected to construct an accurate series of Foraminifera depth biofacies in the San Diego area. It is believed, however, that the material studied gives a general picture of the depth ranges. There do not appear to be any marked general boundaries between faunas at any depths, but rather a series of minor depth range boundaries characterized by upper or lower limits of individual species. On the other hand, there is considerable difference between the fauna from the shallow ends of the traverses and the fauna which occurs in the floor of the San Diego Trough. The boundary between these two assemblages is an indistinct, gradational one and is approximately between 100 fathoms and 200 fathoms water depth. Depth ranges of species occurring in the core sands from the San Diego area are summarized in the species lists for the cores (figs. 1–6). A detailed analysis of the ecology of Foraminifera from the San Diego area is now underway, and the ecologic and taxonomic information presented here is thus subject to modification after further study.

Distributions in Core Sands

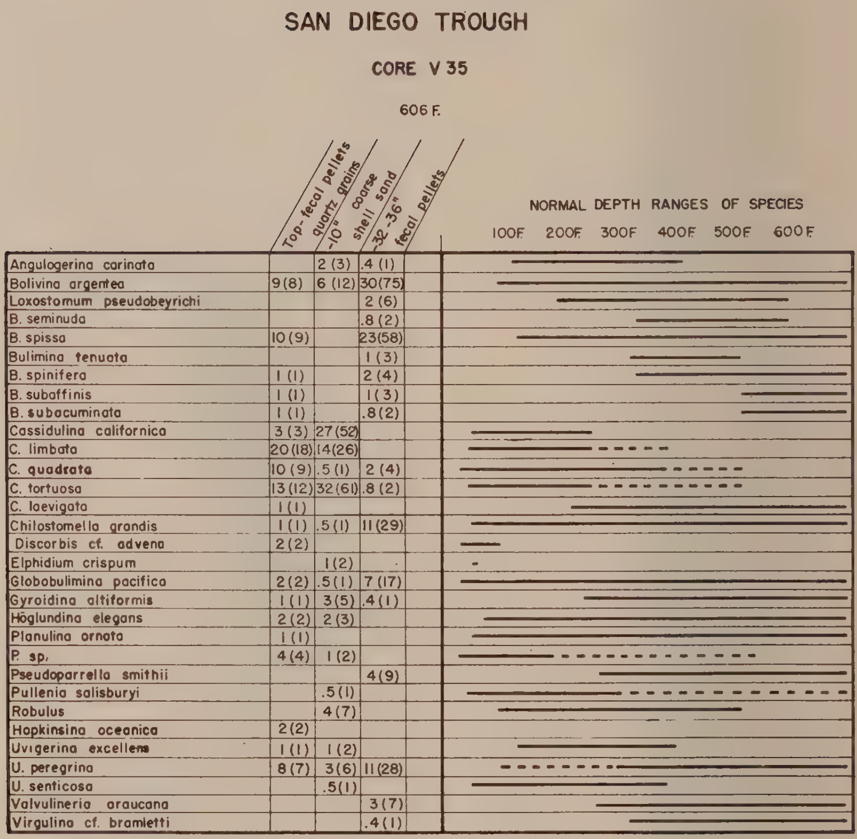
Several sand layers present in cores from the San Diego Trough were examined for Foraminifera, and occurrences of benthonic Foraminifera in some of these sands are listed in figures 1–6. A generalized depth range line is shown at the right of each figure, based on study of the additional material mentioned above. The positions of these cores in the San Diego area are shown on the general chart of the area by Shepard (this symposium, fig. 2, p. 56).

One of the most interesting cores from this area is from station V 35, collected from Coronado Canyon axis near the eastern edge of the San Diego Trough at a depth of 606 fathoms. Figure 1 lists the faunas from three levels in this core. The material other than Foraminifera in the top sample is mud, fecal pellets, and a few quartz grains. The sample at −10 inches consists of broken shell fragments and angular quartz grains up to more than 1 mm in diameter. The sediment at −32 inches to −36 inches is mud and fecal pellets.

The most striking of these three samples is the shell sand at −10 inches, because it is not the type of sediment expected at this depth of water. The fauna of this sample is dominated by *Cassidulina californica*, *C. limbata*, and *C. tortuosa* which live in abundance at depths not greater than approximately 100 to 200 fathoms. There are no species present which are confined to deep water. Deep-water species do occur in the samples above and below the shell sand. The shell sand fauna is characteristic of water depths much shoaler than the depth at which it was collected, and it must have moved down slope to its present position. It is suggested that this sediment came from a depth not greater than about 200 fathoms and probably somewhat shoaler. It appears that the sediment moved more or less as a mass which retained most of its original sedimentary and faunal integrity.

The lower sample in core V 35, at −32 inches to −36 inches, contains essentially a pure deep-water fauna dominated by *Bolivina argentea* and *B. spissa*, and also containing an abundance of *Chilostomella grandis*, *Globobulimina pacifica*, *Uvigerina peregrina*, and *Pseudoparrella smithi*.

The top fauna of core V 35 clearly is a mixed fauna containing significant quan-



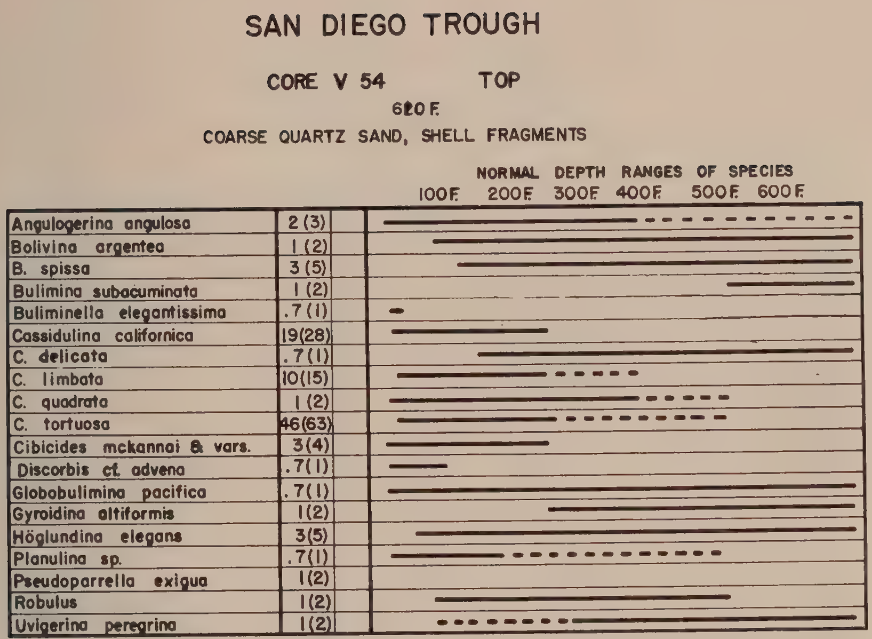
	Top- fecal pellets quartz grains	-10" coarse shell sand	-32-36" fecal pellets	
Angulogerina carinata		2 (3)	.4 (1)	
Bolivina argentea	9 (8)	6 (12)	30 (75)	
Loxostomum pseudobeyrichi			2 (6)	
B. seminuda			.8 (2)	
B. spissa	10 (9)		23 (58)	
Bulimina tenuata			1 (3)	
B. spinifera	1 (1)		2 (4)	
B. subaffinis	1 (1)		1 (3)	
B. subacuminata	1 (1)		.8 (2)	
Cassidulina californica	3 (3)	27 (52)		
C. limbata	20 (18)	14 (26)		
C. quadrata	10 (9)	.5 (1)	2 (4)	
C. tortuosa	13 (12)	32 (61)	.8 (2)	
C. laevigata	1 (1)			
Chilostomella grandis	1 (1)	.5 (1)	11 (29)	
Discorbis cf. advena	2 (2)			
Elphidium crispum		1 (2)		
Globobulimina pacifica	2 (2)	.5 (1)	7 (17)	
Gyroidina altiformis	1 (1)	3 (5)	.4 (1)	
Höglundina elegans	2 (2)	2 (3)		
Planulina ornata	1 (1)			
P. sp.	4 (4)	1 (2)		
Pseudoparrella smithii			4 (9)	
Pullenia salisburyi		.5 (1)		
Robulus		4 (7)		
Hopkinsina oceanica	2 (2)			
Uvigerina excellens	1 (1)	1 (2)		
U. peregrina	8 (7)	3 (6)	11 (28)	
U. senticosa		.5 (1)		
Valvulineria araucana			3 (7)	
Virgulina cf. bramletti			.4 (1)	

FIG. 1.—Foraminifera in 3 samples from core V 35, San Diego Trough. First number for each species is percentage of benthonic fauna, second number is actual number of specimens.

tities of the shallow-water *Cassidulina* species and *Discorbis*, along with deep-water species.

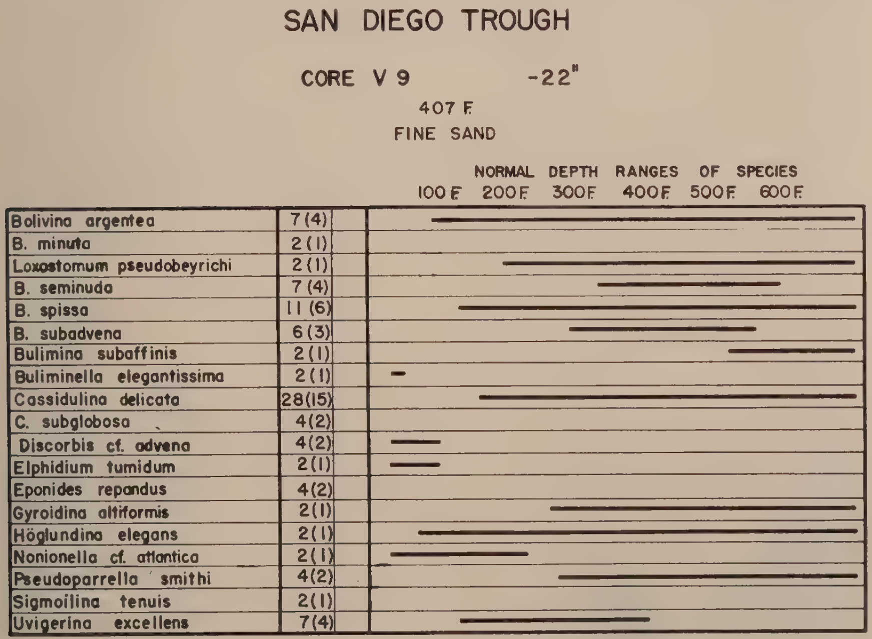
Core V 54 (fig. 2), also obtained in Coronado Canyon, came from a depth of 610 fathoms and from about one-quarter mile south of core V 35. The sediment at the top of this core is a quartz sand containing shell fragments. This sediment contains a mixed fauna, having both shallow-water and deep-water species. Shallow-water origin of the sediment is shown by the abundance of *Cassidulina californica*, *C. limbata*, and *C. tortuosa*, and also by *Buliminella elegantissima* and *Discorbis*. Deep-water species are present, such as *Bolivina spissa*, *Bulimina subacuminata*, *Cassidulina delicata*, and *Gyroidina altiformis*.

Another example of faunal mixing is seen in a fine sand in core V 9 at −22 inches (fig. 3). This core comes from a somewhat shallower depth, 407 fathoms, on the east flank of the San Diego Trough and probably in La Jolla Submarine Canyon. The fauna in this sand is mostly a deep-water one, as shown by the abundance of *Cassidulina delicata* and *Bolivina spissa* and the presence of *Pseudoparrella smithi*. Shallow-water affinities are shown by *Buliminella elegantissima*, *Discorbis* sp., *Elphidium tumidum*, and *Nonionella*



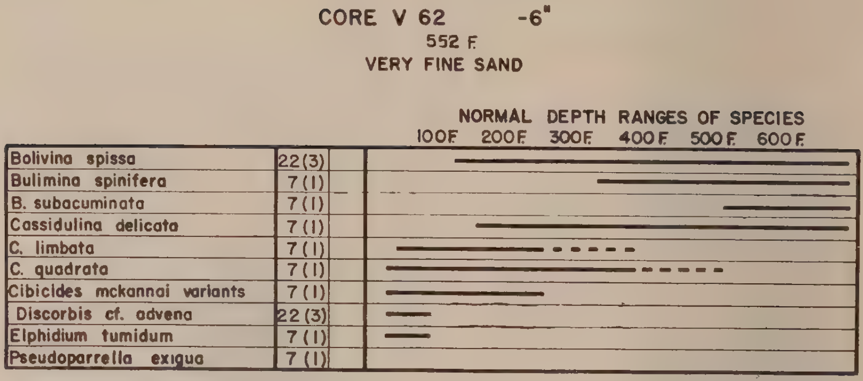
Angulogerina angulosa	2 (3)
Bolivina argentea	1 (2)
B. spissa	3 (5)
Bulimina subacuminata	1 (2)
Buliminella elegantissima	.7 (1)
Cassidulina californica	19(28)
C. delicata	.7 (1)
C. limbata	10(15)
C. quadrata	1 (2)
C. tortuosa	46(63)
Cibicides mckannai & vars.	3 (4)
Discorbis cf. advena	.7 (1)
Globobulimina pacifica	.7 (1)
Gyroidina altiformis	1 (2)
Höglundina elegans	3 (5)
Planulina sp.	.7 (1)
Pseudoparrella exigua	1 (2)
Robulus	1 (2)
Uvigerina peregrina	1 (2)

FIG. 2.—Foraminifera at top of core V 54, San Diego Trough. First number for each species is percentage of total benthonic fauna, second number is actual number of specimens.



Bolivina argentea	7 (4)
B. minuta	2 (1)
Loxostomum pseudobeyrichi	2 (1)
B. seminuda	7 (4)
B. spissa	11 (6)
B. subadvena	6 (3)
Bulimina subaffinis	2 (1)
Buliminella elegantissima	2 (1)
Cassidulina delicata	28(15)
C. subglobosa	4 (2)
Discorbis cf. advena	4 (2)
Elphidium tumidum	2 (1)
Eponides repandus	4 (2)
Gyroidina altiformis	2 (1)
Höglundina elegans	2 (1)
Nonionella cf. atlantica	2 (1)
Pseudoparrella smithi	4 (2)
Sigmoilina tenuis	2 (1)
Uvigerina excellens	7 (4)

FIG. 3.—Foraminifera in core V 9 at −22 in., San Diego Trough. First number for each species is percentage of total benthonic fauna, second number in brackets is actual number of specimens.



Bolivina spissa	22(3)
Bulimina spinifera	7(1)
B. subacuminata	7(1)
Cassidulina delicata	7(1)
C. limbata	7(1)
C. quadrata	7(1)
Cibicides mckannai variants	7(1)
Discorbis cf. advena	22(3)
Elphidium tumidum	7(1)
Pseudoparrella exigua	7(1)

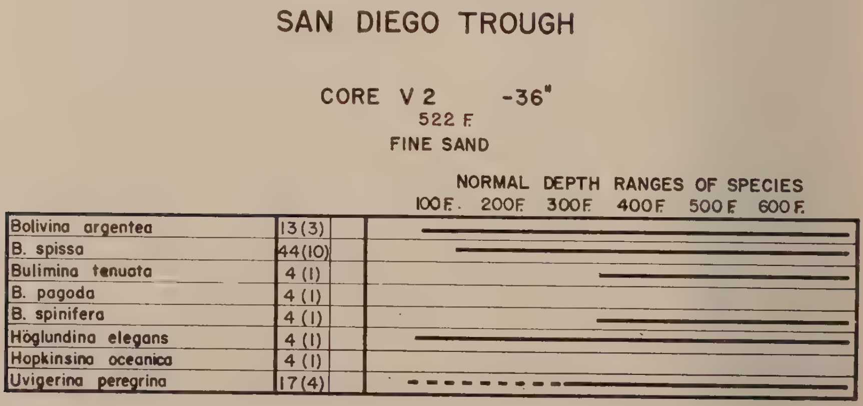
FIG. 4.—Foraminifera from core V 62 at −6 in., San Diego Trough. First number for each species is percentage of total benthonic fauna, second number is actual number of specimens.

cf. *atlantica.*

Fine sand occurs at −6 inches in core V 62 from the San Diego Trough west of La Jolla Canyon, seaward from core V 9 and in deeper water (552 fathoms). This sand also contains a mixed fauna, as can be seen by examining the normal depth ranges of the species (fig. 4). The fauna in this sand is ecologically the same as the fauna in the sand at station V 9, but there are two important differences. There are fewer species and fewer specimens in the sand of V 62 than in V 9.

The sand at −36 inches in core V 2 (fig. 5), from the gentle east slope of the San Diego Trough a little north of La Jolla Canyon, contains a pure deep-water fauna, as can be seen by examining the normal depth ranges of the species. If this sand originated in shoal water, as all the evidence in this area indicates, then it has lost any faunal evidence of its shallow-water origin.

The faunas in core sands from stations V 90 and V 115 are of interest in this connection. These come from near the west side of San Diego Trough. Both sands contain a pure deep-water fauna



Bolivina argentea	13(3)
B. spissa	44(10)
Bulimina tenuata	4(1)
B. pagoda	4(1)
B. spinifera	4(1)
Höglundina elegans	4(1)
Hopkinsina oceanica	4(1)
Uvigerina peregrina	17(4)

FIG. 5.—Foraminifera from core V 2 at −36 in., San Diego Trough. First number for each species is percentage of total benthonic fauna, second number is actual number of specimens.

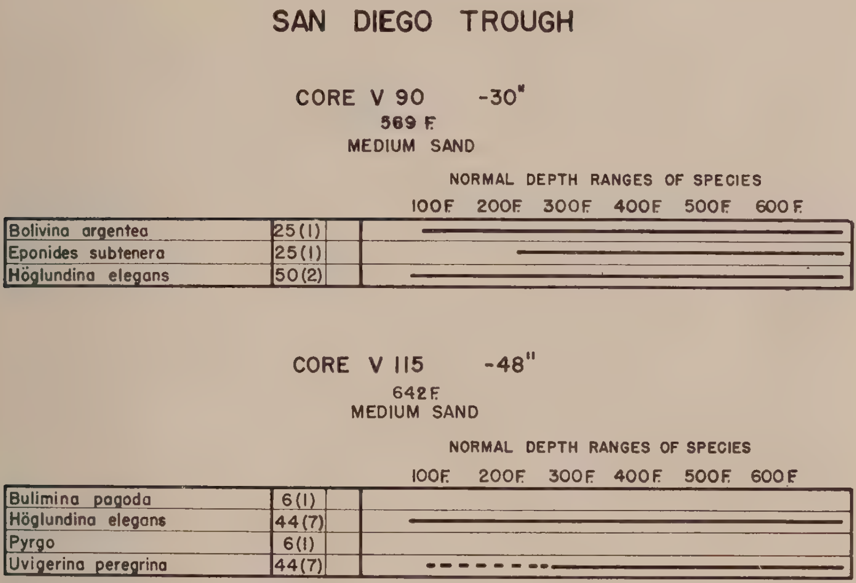


FIG. 6.—Foraminifera from sand layers in cores V 90 and V 115, San Diego Trough. First number for each species is percentage of total benthonic fauna, second number is actual number of specimens.

and both contain very few species (fig. 6). In addition, the sand at V 90 is striking because it contains so few specimens of Foraminifera. Small numbers of specimens also is characteristic of the other two sands containing only deep-water Foraminifera, but it is not as striking as at station V 90.

BENTHONIC FORAMINIFERA IN TWO CORES FROM THE SIGSBEE DEEP

Figure 7 shows distribution of benthonic Foraminifera in cores 335 and 336 from the Sigsbee Deep in the Gulf of Mexico. These cores came from water depths of approximately 2,000 fathoms. Each core was somewhat longer than 2 m in length. Representative samples are listed with the depth in cm within the core at the top of the figure, and the benthonic Foraminifera are given as per cent of total benthonic Foraminifera in each sample. Modern depth ranges of the species occurring in these cores are shown, and are based on a study of the ecology of Foraminifera in the northwest Gulf of Mexico by the writer (MS., in press). Species are described and illustrated by Phleger and Parker (MS., in press).

The fauna in the upper parts of cores 335 and 336 is dominated by *Planulina wuellerstorfi* and *Pseudoparrella decorata. Pseudoparrella decorata* is confined at present to depths greater than 550 fathoms, and *Planulina wuellerstorfi* only occurs deeper than about 275 fathoms. *Eponides tumidulus*, which is also present, occurs only deeper than about 550 fathoms. Other species in these upper core sections also occur in the deep-water assemblage of the Gulf of Mexico and this upper fauna is characteristic of the depth at which it was found (2,000 fathoms). These upper faunas occur in a muddy *Globigerina* ooze and are postglacial in age, based on the distribution of the planktonic fauna.

The lower faunas in cores 335 and 336 occur in a fine-grained sand which is not

ANALYSIS OF BENTHONIC FORAMINIFERA

FROM 2 SIGSBEE DEEP CORES

	CORE 335 1880 F																		CORE 336 1930 F									
Cm from top of core	0	8	24	36	56	80	105	120	138	152	156	168	178	182	186	193	198	214	1	28	41	96	117	133	153	168	189	204
Angulogerina bella													2			1	2								2			
Bifarina decorata																3	4									2		
Bigenerina irregularis																1								2				3
Bolivina alata															21										5	5	3	
B. albatrossi																	2							4				
B. barbata																5	3								2		3	3
B. lowmani																	8										5	
B. striatula var. spinata													5			3	2											
B. subaenariensis var. mexicana																3	5								5		11	
Bulimina aculeata																	1							13	5		5	8
B. affinis										9	7	20	10	17	36								15	4	2	2	3	3
B. alazanensis																3	2							2				3
B. marginata													2			3	2									5		
B. striata var. mexicana													2			1	3										3	5
Cancris oblonga																								2	2			
Cassidulina laevigata var. carinata													2			5	2							2		7	3	3
C. subglobosa			1	2				4								1											5	
Cibicides concentricus																3	6							4	5	10	11	13
C. aff. floridanus	3			2			3																	4	5	2		5
Eggerella bradyi	5	2		3	5	8	5	4	4	2	4							4			6	3	6					
Elphidium discoidale													5			31	2[illegible]							18	25	20	8	30
E. cf. fimbriatulum																	1							2				
E. gunteri var. galvestonense																1	1							4	5		3	
Eponides polius	14	12	17	26	5	1													21									
E. tumidulus	3	2		5	9	11	5		8	2										11	12	14						
E. umbonatus					5	9	10	2	4	7	7										6	3	9	2		2	3	
Glomospira charoides	25	10	1																5	11	6	3						
Gyroidina soldanii var. altiformis								6	4												12	3				2	3	
Nonion pompilioides	5	12	20	14	19	14	13	2	14	9	11	20						4	5	11		7	6					3
Nonionella atlantica																	3							2	2	2		
Parrella cultur			1		2	1										1												
Planulina wuellerstorfi	11	38	31	12	21	23	15	31	32	30	33			5			1	12	47	33	6	11	36			2	5	
Pseudoparrella (?) decorata	8	10	7	23	19	3	13	19	18	7	7			5		1		4		22	35	21	12	2				
Reussella atlantica													7		7	1								4	2			5
Rotalia beccarii var. parkinsoniana																8	9							4	7	7	3	3
R. beccarii var. tepida																								2		2		
R. translucens													2												2			3
Uvigerina peregrina													10	5		5	6							11	2	12	11	5
U. peregrina var. parvula															21		2											
Virgulina pontoni													5	11			2								2	2		

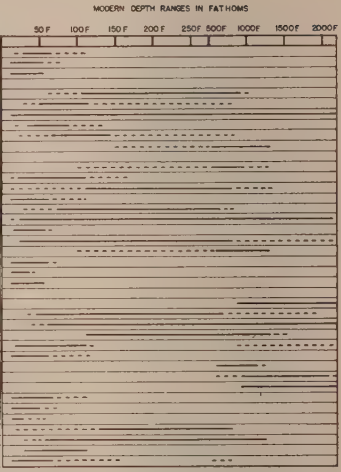


FIG. 7.—Foraminifera in selected samples from cores 335 and 336, Gulf of Mexico. Numbers are percentages of total benthonic population for each sample.

being deposited in this area at the present time. This material is presumed to be of late glacial age on the basis of the planktonic fauna. The lower core benthonic fauna is dominated by *Elphidium discoidale* which occurs not deeper than about 65 fathoms in the modern fauna. Other species in the lower core fauna which are at present restricted to depths less than approximately 50 fathoms are *Bifarina decorata*, *Bigenerina irregularis*, *Cibicides concentricus*, *Elphidium* cf. *fimbriatulum*, *E. gunteri* var. *galvestonense*, *Rotalia beccarii* var. *parkinsoniana*, and *R. beccarii* var. *tepida*. The following species occur only shoaler than approximately 110 fathoms; *Angulogerina bella*, *Bolivina striatula* var. *spinata*, *Cancris oblonga*, *Nonionella atlantica*, and *Uvigerina peregrina* var. *parvula*. The following species are only known from intermediate depths: *Bulimina aculeata* occurs from about 150 fathoms to 1,100 fathoms, but is most abundant between about 275 fathoms and 1,100 fathoms. *Bulimina alazanensis* extends from about 100 fathoms to 1,100 fathoms but is most abundant between 275 fathoms and 700 fathoms. Some of the other species in this fauna have various deep limits to their range. The following species limited to depths greater than about 550 fathoms also occur in this lower fauna; *Planulina wuellerstorfi* and *Pseudoparrella decorata*.

The abundance of specimens at present restricted to water depths less than 50 fathoms, indicates that the fine sand must have originated in depths less than 50 fathoms. The mixture of species from all ranges of depth seems to prove that the sand containing the lower faunas moved down slope from shoal water to its present depth at 2,000 fathoms. The presence of deep-water species in these lower faunas indicates that the water depth when the sand was deposited at these localities was about the same as at present, and certainly greater than 550 fathoms.

These cores were taken from the western part of the Sigsbee Deep from a few miles beyond the lower part of the continental slope. It is at least 80 nautical miles from core 335 to the nearest depth of 50 fathoms in this area, suggesting that the sand containing the lower core fauna moved at least this distance. Station 336 is 25 miles seaward from station 335 and this gives a total horizontal movement of approximately 105 nautical miles. The cores at station 337, 25 miles seaward from station 336, and core 334, 25 miles landward from station 335, did not contain this shallow-water fauna in any section.

DISCUSSION

The faunal evidence presented is considered to be proof that the deep-sea sands discussed have moved from shoal into deep water. The faunal data suggest somewhat different kinds of movement in sands having different faunal constitutions. It should be possible to trace certain details of the history of one of these displaced sands, using benthonic Foraminifera as guides. This can be accomplished, however, only if sufficient data are available on the ecology of benthonic Foraminifera and if the behavior is known of tests of the Foraminifera in transportation and deposition of an enclosing sand. These data are incomplete, but there is sufficient information to make tentative suggestions.

The shell sand at −10 inches in core V 35 contains pure shallow-water fauna which is not characteristic of the relatively deep water in which it was found. It appears that this material was deposited as a mass, without mixing with other sediment, on a surface of mud containing a Foraminifera fauna characteristic of the depth at which it is found. The movement of the shell sand occurring at −10 inches may have been similar to that of a small landslide without significant internal turbulence. The absence of deep-water species also suggests that this sand was covered before the normal deep-water Foraminifera could populate the area. It seems reasonable that repopulation of an area covered by foreign sediment would require only a short time. It is probable that the material at the top of the core was part of the same mass movement of sediment and covered the shell sand.

The muddy sand at the top of core V 35 contains both shallow and deep-water species which could occur together by physical mixing of the sediment and/or by population of the sediment originating in shallow water by deep-water species. It is possible that this upper part of the sediment represents the turbulent part of the material which moved down slope and that there was physical mixing. Population by deep-water species must have occurred subsequently to deposition regardless of whether there was previous mixing. A sand at the top of core V 54, taken within about one-quarter mile of core V 35, also contains a fauna having shoal and deep-water species. This may represent the edge of the same mass of sand which originally moved down slope as a turbidity current. It is expected that there may be turbulence around the edges of the sediment moving in this manner and some contamination with foreign sediment.

It appears that many of the other mixed faunas from the San Diego Trough were due to population with deep-water species after deposition of the sand in the new environment. The sand in core V 9 on the east flank of San Diego Trough may be used as an example. It is probable that this sand came from shallow water carrying with it specimens of shallow-water Foraminifera, approximately in the same frequency as they are found in similar sands in shoal water. Inclusion of the deep-water specimens could be accomplished by either or both of two methods. Physical mixing of the sediments and, therefore, of the faunas is possible. This does not seem likely in the V 9 sand, however, because it is well-sorted (So—1.26) and undoubtedly came from a single source and depositing agency. It seems more probable that the sand was populated by the normal deep-water Foraminifera after deposition at its present position.

It is possible that some of the deep-water sands may have moved down slope to their present positions in more than one stage. A sand with such a history would be expected to add to its Foraminifera fauna by population of the surface at each intermediate stop. This would require that the surface of the sand remain uncovered by other sediment for the time necessary for the local Foraminifera to invade the material. If sufficient information is obtained on the Foraminifera ecology in the San Diego region, it should be possible to discover such a history. The poor sorting in the sand at −48 inches in core V 115 (So—2.94) suggests a complex history for this sand.

The lower benthonic fauna in the two cores from the Sigsbee Deep also suggests a complex history for the sands in which they are contained. The Foraminifera clearly came from all ranges of depth, from less than 50 fathoms to more than 550 fathoms. The faunal mixing could be accomplished by down slope movement in a series of short stages, by mixing of sediment during one movement, or by supply of sediment from several sources and depths. Core 336 is from the relatively flat floor of the Sigsbee Deep, and more than 25 nautical miles from the base of the continental slope. Occurrence of sand with shoal-water Foraminifera at this position indicates that sediment moving downslope may be carried out onto a relatively flat basin well beyond the base of the slope where it obtained its momentum. It seems likely that sediment of mud sizes may be carried much farther than sand and deposited widely over an ocean basin.

There is little doubt that the lower faunas in cores 335 and 336 are age correlatives, being of latest glacial age. Age determination is based upon the vertical sequence of relatively warm-water and cold-water planktonic Foraminifera within the cores. This age correlation indicates that the sands containing the shallow-water benthonic fauna in the cores probably were deposited by the same turbidity current. The dimensions of this movement of sediment are thus approximately defined since the sand deposit appears to cover an area at least 25 miles in one direction, although there is no assurance that the sand is continuous between the two stations.

One group of deep-water sand samples from the San Diego Trough contains a pure deep-water fauna, at stations V 2, V 90, and V 115. It is probable that these sands are of shallow-water origin as well as the sands which contain some shallow-water species. It is suggested that the shallow-water specimens originally present may have been segregated from the sand in these samples by differential sorting of the sedimentary material and the sediment was devoid of Foraminifera when it was deposited. The specimens originally present either may have been left behind during the movement or were carried elsewhere and deposited. The two samples came from near the western side of the trough, and thus at some distance from a probable source of the sand; this may add circumstantial evidence to the argument for differential sorting. If this has happened, it indicates a somewhat different process of deposition than in samples containing a mixed fauna.

Differences in relative sizes of total populations in deep-water sands containing only a deep-water fauna may be due to rate of burial of the sand. A very small population in a large sample, as in the sand at −30 inches in core V 90, may indicate that the sand was buried before a larger population had time to invade the exposed surface of the sand.

These deep-water sands do not cover large areas with a continuous layer of sand, but have local distributions. This is illustrated in the western part of the Sigsbee Deep where no other nearby core material examined contained evidence of shallow-water origin. Surveys in the San Diego Trough by Shepard and Ludwick (personal communication) have shown similar discontinuous distributions. Another feature of these deep-water sands containing shallow-water Foraminifera is that they occur in a variety of areas having a wide geographic distribution, as shown by Shepard (this symposium, pp. 53–65). There are several less-striking examples of displaced faunas from parts of the northwestern Gulf of Mexico other than in the small area already discussed. These are contained in core faunas collected during a reconnaissance of the northwestern Gulf of Mexico made in 1947 and to be reported elsewhere (Phleger, MS., in press). Two deep-sea cores collected by the Swedish Deep Sea Expedition, and now being studied, have sands containing shallow-water Foraminifera. One of these cores, from approximately 500 nautical miles off the Amazon and 350 miles from the edge of the continental shelf, contains specimens of *Rotalia beccarii* var. *parkinsoniana*, a valid continental shelf species. A core from south of Marjorca in the western Mediterranean contains a fauna which is clearly of shoaler water origin than the depth at which the core was collected; it is not possible to give more specific information on this core because there are few data on distribution of Mediterranean Foraminifera.

SUMMARY OF CONCLUSIONS

Shallow-water Foraminifera occurring in deep-sea sands are evidence that these sands have been displaced from shallower depths by turbidity currents or other mechanisms. Deep-sea sands having only shallow-water species are believed to have moved down slope as a unit, without contamination from other sediment. The presence of both shallow and deep species suggests either mixing of the sediment or population by deep-water Foraminifera afer deposition of sand in deep water. Deep-sea sands containing only deep-water species may have lost shallow-water specimens originally present by differential sorting during transportation and deposition. The size of the population of Foraminifera in deep-sea sands may be an indication of how quickly these sands were buried. Faunas in deep-water sands from the Sigsbee Deep suggest movement from 50 fathoms to 2,000 fathoms over a distance of at least 105 miles. Some of the sands may have come from more than one source and some may have gone through several stages of downslope movement to their present position.

Deep-water sands cover only small areas but are reported from many parts of the world. It is believed that they are of common occurrence.

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Vol. 64, pp. 129-130 November 19, 1951

PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY OF WASHINGTON

ALLOSEBASTES, NEW SUBGENUS FOR SEBASTODES SINENSIS, SCORPAENID FISH OF THE GULF OF CALIFORNIA[1]

By Carl L. Hubbs

The species of *Sebastodes* that Gilbert (Proc. U. S. Nat. Mus., vol. 13, 1890, pp. 81-82) described from the Gulf of California as *Sebastichthys sinensis* is so distinct as to warrant its separation as the type and sole member of a new subgenus.

Allosebastes, new subgenus

The most notable character of this subgenus is the reduction of the anal soft-rays to 5—the number characteristic of *Scorpaena* and of most other tropical genera (Barnhart and Hubbs, Bull. Scripps Inst. Oceanogr. Univ. Calif., vol. 5, 1946, p. 373). As is often true, the value of this character lies in its consistency rather than in the amount of difference. The tropical genera normally with 5 anal soft-rays very seldom deviate from that number and all of the many other species of *Sebastodes*, with rare individual exceptions, have 6 to 14 anal soft-rays, usually 6, 7, 8, or 9 (Jordan and Evermann, Bull. U. S. Nat. Mus., no. 47, pt. 2, 1898, pp. 1765-1835; Matsubara, Trans. Sigenkagaku Kenkyusko, vol. 1, 1943, p. 97).

The other fins have a ray formula that is normal for the genus *Sebastodes:* dorsal, XIII, 12 (rather low but not uniquely so in number of soft-rays); caudal, 7 + 7 (principal rays); pectoral, i, 9, vii = 17 in each fin; pelvic, I, 5. The pertinence of the species to *Sebastodes* or to a very closely related segregate is confirmed by such characters as the scaly, only moderately spiny and little distorted head, the posteriorly narrowed, unkeeled and unspined suborbital stay, the complete dentition, and the normal fins. The definite though thick and blunt intromittent organ of the male is similar to that of the species of *Sebastodes*, all of which, so far as known, bear prolarvae.

Other more or less extreme though less trenchantly distinct characters of *S. sinensis* are the smooth, mostly cycloid scales; the unswollen lower pectoral rays; the excessively long anal spines (the second extends well beyond the longest soft-rays, the third almost reaches the tip of the longest soft-ray); the closely clumped subparallel upper 3 preopercular spines (the lower 2 are well separated and divergent); the protuberant posterior end of the mandible, almost resembling a flat spine; and, especially, the very firm, well-exposed suborbital stay (second suborbital), with the bone widened about the unusually large pore, which has a somewhat raised and roughened rim.

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[1] Contributions from the University of California, Scripps Institution of Oceanography, New Series, No. ~~000.~~ 546

The general distinctiveness of this species, as well as its reduced number of anal rays, is correlated with its restriction to the essentially tropical fauna of the Gulf of California, where it alone represents this speciose genus of the North Pacific (Jordan and Evermann, *l. c.*, 1898, pp. 1765-1835; Matsubara, *l. c.*, vol. 2, 1943, pp. 175-252, under *Sebastes*). Except for one species or species-complex ranging from Perú to South Africa, the entire genus is otherwise confined to the more temperate and to the boreal waters of the North Pacific (Hubbs, Pac. Sci., vol. 4, 1950, p. 70). The disjunction of populations, both in the Southern Hemisphere and in the Gulf of California, presumably dates from some Pleistocene period of oceanic cooling (Hubbs, Jour. Mar. Res., vol. 7, 1948 (1949), p. 463). There were presumably several such periods of cooling and *Sebastodes sinensis* has probably been separated from its congenors since middle or early Pleistocene time.

It is not wholly clear, however, that *Sebastodes* (*Allosebastes*) *sinensis* represents an offshoot from *Sebastodes*, with the number of anal rays independently reduced. A thorough revision of the American species, with attention to such anatomical details as Matsubara (*l. c.*, 1943, vols. 1-2) used in his study of the species of the western Pacific, will be required before the phyletic position of *S. sinensis* can be interperted with confidence. It may represent a group, or stage of evolution, now largely extinct, that is transitional between the temperate and the tropical genera, or *vice versa.* It may be shown to be so distinct as to warrant full generic separation. In some respects it resembles *Helicolenus*, from which it differs at least in the unkeeled suborbital stay and in the number of dorsal spines, 13 rather than 12 (a distinction of great significance in this group, because of the consistency of the difference). From each of the few genera with 13 dorsal spines and 5 anal soft-rays, as well as from all other genera except *Sebastodes*, as these were distinguished by Matsubara, *S. sinensis* differs in several characters of acknowledged generic import.

Not having examined the species and not having noted its more distinctive features, classifiers of *Sebastodes* have variously interpreted the relationships of *S. sinensis* in the large complex of species. Eigenmann and Beeson (Am. Nat., vol. 27, 1893, p. 670) classed it, along with a miscellaneous assortment of other species, in their new genus *Pteropodus.* Cramer (Proc. Calif. Acad. Sci., ser. 2, vol. 5, p. 600) associated it in his key with *zacentrus, elongatus, levis* and *rubrivinctus,* leaving all in *Sebastodes* without even subgeneric separation. Jordan and Evermann (Rept. U. S. Comm. Fish and Fish., 1895 (1896), p. 431 and Bull. U. S. Nat. Mus., no. 47, pt. 2, 1898, p. 1776), essentially adopting Cramer's arrangement, combined *sinensis* with the 4 species just named in their new subgenus *Hispanicus.*

This note is based on a recent examination of the holotype of *Sebastichthys sinensis* (U.S.N.M. No. 43085). Only the holotype and 1 paratype have been collected, both at Albatross Station 3015 in the Gulf of California, at a depth of 145 fathoms, at 29° 19′ 00″ N. Lat., 112° 50′ 00″ W. Long.

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Reprinted from Biological Bulletin, Vol. 101, No. 3, 274–284, December, 1951
Printed in U. S. A.

PHOSPHATE UTILIZATION BY DIATOMS

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PHOSPHATE UTILIZATION BY DIATOMS[1]

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Routine measurements of inorganic phosphorus concentration are frequently made on standard oceanographic stations to ascertain the potential productivity of marine waters. In quantitative, ecological studies on diatom populations in the Atlantic Ocean, Riley, Stommel and Bumpus (1949) have utilized the phosphate concentration as a nutrient index. Their equation of productivity depends upon the experimental results of Ketchum (1939), who found that phosphate concentrations below 0.55 microgram-atoms per liter limited the growth of *Nitzschia closterium.*

Riley, Stommel and Bumpus (1949) further checked the validity of this index in their photosynthetic rate equation by calculating the phosphate requirements of a growing plankton population, assuming that 100 carbon atoms to one atom of phosphorus are needed for normal metabolism. However, in studies on the fresh water diatom *Asterionella formosa,* Lund (1950) found that the phosphate content of the plant varied by a factor of seventy in both natural and cultural populations. He stated that the cells are able to store phosphorus in excess of their immediate requirements even at very low levels of phosphate concentration.

The data on the amount of phosphate contained in marine phytoplankton, as found by Ketchum and Redfield (1949), show considerable variation, making the determination of phosphate requirement difficult and uncertain. The use of phosphate as a parameter in the computation of productivity would appear to be premature therefore, until such time as definitive values of the phosphate requirement shall have been established. Even then the total mineral requirements relative to one another must be known and their seasonal and geographic abundances must be shown to vary with biological activity. The use of an arbitrary and easily measured nutrient index for correlation with diatom abundances seems to be unwarranted.

The release of phosphate by marine plankton is an important factor in ecological investigations. Cooper (1935) found that one-fourth to one-half of the phosphate added as phytoplankton in sea water was set free to the environment as inorganic phosphate after one month. Seiwell and Seiwell (1938) reported similar results.

Because of the scarcity of experimental data on the uptake of phosphate and its subsequent release from diatoms, controlled experiments using radioactive phosphate as a tracer were devised to follow the path of phosphate quantitatively from the marine environment to the plant as a function of time. This present study initiates a series of investigations which will attempt to determine by modern radiochemical techniques the minimal quantities of mineral nutrients needed for optimal growth and multiplication of a diatom species in culture.

[1] Contribution from the Scripps Institution of Oceanography, New Series No. 547.

LABORATORY TECHNIQUES

Stock cultures

Single cells or colonies of cells were isolated from inshore water samples taken at the pier of the Scripps Institution of Oceanography, La Jolla, California. Isolated cells of a given species were washed by passing through three drops of sterile nutrient sea water medium, and were then placed in 10 ml. of medium in a test tube. When the diatom population had reached approximately 1000 cells per ml., a one-ml. aliquot was transferred to a cotton-stoppered 250-ml. Erlenmeyer flask containing 100 ml. of a sterile nutrient sea water medium, as described below. Cultures were maintained by transferring one ml. of culture to a flask of fresh medium at two-week intervals. The original cells of the *Asterionella japonica* culture used in the early part of the work had been isolated from the plankton sample in the fall of 1948; the initial cells of the *Asterionella japonica* later utilized were isolated from the plankton samples in the winter of 1950.

Preparation of the nutrient sea water medium

A basic requirement in the radiochemical assay of the partition of phosphate between the nutrient medium and the diatoms is that the total phosphate be contained only within these two fractions. Thus, any phosphate precipitation during the preparation of the enriched sea water or during the course of the experiments invalidates the measurements. Microscopic examination of culture waters prepared in the normal way revealed particulate matter which was found by chemical analysis to be iron phosphate. This solid phase was able to adsorb and to contain a considerable portion of the phosphate. Since the cells often clung to, or were entrapped, or covered by these masses, these precipitates tended to obscure the diatom cells during visual counting, making the counting more difficult. Therefore, the sea water collected for use in the culture medium was subjected to special treatment before and during enrichment to prevent any formation of particulate matter.

The sea water used in the preparation of the medium was collected in glass containers, approximately 14 liters at a time, from the pier. It was filtered through either S & S No. 489 Blue Ribbon or Whatman No. 42 paper before enrichment with nutrients.

The medium used was a modification of Allen and Nelson's (1910) culture solution (Table I). The sea water and the nutrients were sterilized in separate containers. The salts were sterilized in two portions: one, a combination of the KNO_3, $MnCl_2$, and Na_2HAsO_4; the other, the phosphate made up to 100 ml. of

TABLE I

Culture medium nutrients

Solution		Amount of solution added per liter
M/10	KNO_3	20 ml.
M/100	$MnCl_2$	0.1 ml.
M/100	$CoCl_2$	0.1 ml.
M/100	Na_2HAsO_4	0.1 ml.
3M/1000	K_2HPO_4	Varied through investigation
M/10	Ferric citrate	0.1 ml.

solution with distilled water. The sea water was also sterilized in two portions of three liters each in 4-liter reagent bottles. Sterilization was achieved in the autoclave at 120° C. and 18 pounds pressure. Exposure times were 10 minutes for the salts and 25 minutes for the sea water. After cooling, the water and salt solutions were combined in a sterile 9-liter serum bottle, the salt solution entering through a separatory funnel as the sea water simultaneously passed through glass tubing to the bottom of the bottle. The KNO_3 combination was added with the first three liters of sea water, and the phosphate with the second portion of the sea water. The iron citrate solution was added directly to the culture bottles before diatom inoculation.

Bio-assay

Water samples sometimes failed to produce growth in spite of enrichment. To avoid cultural failures, all of the water collected was first assayed. After preparation of the enriched water, a sample was drawn and placed in several stock culture flasks and then inoculated. An initial count was made and the cultures re-counted twice at weekly intervals. Not infrequently these preliminary assays showed that, in spite of enrichment, the water was refractory to diatom growth. Such water was never used in the radiochemical experiments.

Radiochemical culture techniques

Seven hundred ml. of the enriched sea water was added to the one-liter wide-mouthed culture flasks (Fig. 1), which were stoppered with cotton plugs. The water within the culture bottles was stirred by means of a floating magnetic stirrer made from a 50-ml. round bottom boiling flask. In initial experiments in which the magnetic stirring rod was allowed to rest on the bottom of the culture bottles, the diatoms were destroyed. The solutions were stirred for a period of one minute out of every fifteen minutes with a Haydon Repeat Cycle Timer. It was found that at this stirring rate all of the diatoms received adequate light for normal growth. Continuous stirring resulted in some diatoms clinging to the walls of the glass vessel.

Six such flasks were kept in a constant temperature room at 18° ± 2° C. Five of the flasks contained diatoms while the sixth flask was used as a radiochemical control. The six culture flasks received an equal illumination from a 48-inch, forty-watt fluorescent lamp. The light intensity, as measured with a Weston Photronic Foot Candle Meter, was 55 ± 5 foot candles.

Diatoms were introduced at an inoculation level of about 400 diatoms/ml. Simultaneously, a 10-microcurie aliquot of P^{32} as phosphate ion [2] in sea water was added so that the counting rate of one ml. of the initial solution was about 3000–4000 counts per minute as measured under an end-window Geiger-Muller tube with a window thickness of 1.4 mg./cm.^{2} and a geometry of nine per cent.

Daily radiochemical assays were made on the cultures to determine the phosphate content of the total solution, the diatoms, and the liquid medium freed of diatoms by the following method: one ml. of the whole solution (after continuous stirring for five minutes) was evaporated to dryness under an infrared lamp on a 10

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[2] The radioactive P^{32} used in this investigation was supplied by the Oak Ridge National Laboratory on allocation from the Isotopes Division, U. S. Atomic Energy Commission.

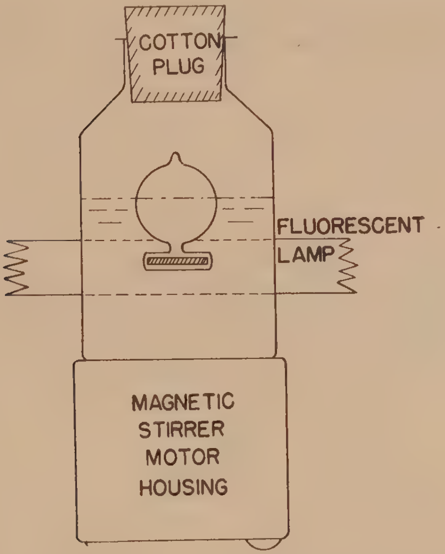

FIGURE 1. The diatom culture bottle. Six such bottles were aligned in front of a single fluorescent lamp for a single experimental run.

cm.^{2} copper planchet. When the activity is plotted as a function of time, the known decay rate of 14.3 days of P^{32} is obtained (Fig. 2). This result indicated that there was no loss of phosphate during the experiment by adsorption on the walls of the glass vessel or by the clinging of diatoms to the walls or bottom of the culture flask. It further revealed that, within experimental error, the volume of diatoms at maximum growth was small with respect to the one-ml. aliquot, otherwise a dilution of the activity with time would have been observed.

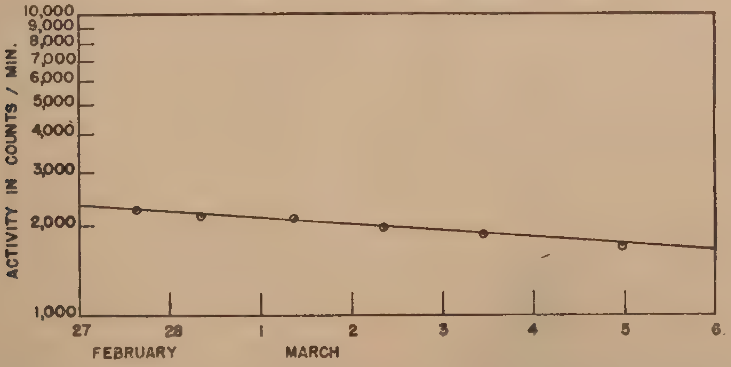

FIGURE 2. The radioactivity of the phosphate in an aliquot of the culture medium containing the diatoms is indicated by the open circles. The theoretical decay of P^{32} is shown by the heavy line. Data from experiment 3T.

Three ml. of the whole solution was centrifuged at 2000 rpm. and one ml. of the supernatant liquid was evaporated to dryness under an infrared lamp on a 10 cm.^{2} copper planchet. The activity of the supernatant liquid, a_s, was assayed under the Geiger-Muller tube and compared to the whole solution, a_t. We thus arrive at the value of phosphate per diatom, P_d, at any given time t, the time of withdrawal of the aliquots from the culture bottles as

$$P_d = \frac{P_t(1 - a_s/a_t)}{N}, \tag{1}$$

where P_t is the initial concentration of phosphate in the culture medium in microgram atoms/ml. and N is the total number of diatoms per ml.

The diatom population assay was made in the following way. One-ml. aliquots were withdrawn from the stirred cultures at the time that the samples for radiochemical analysis were taken. A sufficiently representative population of this

TABLE II

Culture flask	N, cells/ml.		P_s, micro-gram atoms/liter		Growth constant, hours	Final P_d, microgram-atoms $\times 10^8$
	Initial	Final	Initial	Final		
1L	318	122,000	12.8	4.4	15	6.9
2L	612	48,000		4.3	15	8.9
3L	1059	68,000		8.5	17	6.3
4L	450	76,000		5.4	13	9.7
5L	625	68,000		4.5	17	6.6
				Average with std. dev.		7.7 ± 1.5
10	1760	80,000	8.4	4.2	20	5.3
20	1970	40,000		4.4	20	10.1
30	2610	62,000		4.8	20	5.7
40	1320	54,000		4.0	16	8.2
50	1140	40,000		6.4	20	4.9
				Average with std. dev.		6.8 ± 2.2
1T	783	84,000	4.2	0.59	13	4.3
2T	327	72,000		0.57	11	5.0
3T	396	75,000		0.69	11	3.3
4T	420	43,000		0.76	12	7.7
5T	321	40,000		1.22	14	7.5
				Average with std. dev.		5.6 ± 2.0
1W	66	52,000	2.7	0.25	17	3.9
2W	253	30,000		0.25	12	5.0
3W	375	41,000		0.20	12	6.0
4W	429	52,000		0.15	12	4.9
5W	267	45,000		0.22	12	5.7
				Average with std. dev.		5.1 ± 0.8

was counted to obtain the density of the population expressed as cells per ml. Care was taken that the cells counted were normal and healthy. Moribund or dead cells were not numerous except in aged cultures, *i.e.,* in some cultures made in early experiments before the bio-assays were made.

The supernatant liquid of the radiochemical control flask was assayed radiochemically, and its activity was compared with that of the whole solution. Any difference would indicate phosphate precipitation. In all of the experiments the activity of the supernatant liquid and the whole solution of the radiochemical control flask were the same within experimental error.

The phosphate analyses were made by the Wooster and Rakestraw (1951) modification of the method of Deniges-Atkins on the solution before the addition of the radioactive phosphate solution. The maximum concentration of phosphate introduced by this addition was 0.01 micro-gram atoms/liter. The phosphate remaining in solution, P_s, at any time t is given by

$$P_s = (a_s/a_t)P_t. \tag{2}$$

RESULTS

Diatom culture experiments were carried out in media varying in initial phosphate levels from 2.7 to 12.8 microgram-atoms per liter. Table II shows the results found between the diatom populations and the phosphate in solution. Columns 2 and 3 represent the initial and final cell count of the diatoms, the final count representing the population when the first signs of leveling-off appeared in the cultures. It should be noted in column 3 that essentially the same final concentrations of diatoms were obtained in all runs. Columns 4 and 5 represent the initial and leveling-off values of the phosphate remaining in solution. The growth constant, or the time for a given cell to divide, is given in column 6. The final concentration of phosphate per diatom as calculated from equation (1) is given in column 7. It is seen that the final phosphate content of the diatoms and the maximum cell population are essentially independent of either the initial inoculum or the initial phosphate level. The spread in the figures is undoubtedly due to cumulative errors in counting of the diatoms, radiochemical assay and sampling techniques.

If one takes as the phosphate content per diatom 5.0×10^{-8} microgram-atoms per cell and a population of 50,000 cells/ml., it is seen that 2.5 microgram-atoms of phosphate per liter are needed for a further division. In experiments T and W there was not enough phosphate remaining in solution to support much further growth.

The dynamic aspects of the phosphate uptake by diatoms are presented in Figures 3 and 4. Figure 3 depicts the relationship between the phosphate remaining in solution and the population level during an experimental run. It is seen that the point at which the diatoms reached their peak growth coincides closely with the leveling-off of the phosphate uptake at 0.25 microgram-atoms per liter. Evident in Table II, in the four replicate culture flasks of run W, is the leveling-off of the phosphate uptake and diatom growth which occurred at phosphate concentrations in the solution between 0.15 and 0.25 micro-gram atoms of phosphate-phosphorus per liter. It was further found that after the leveling-off period, the phos-

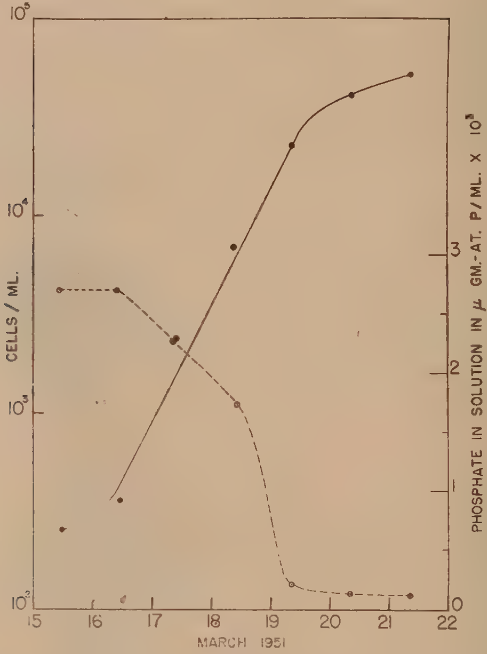

Figure 3. Phosphate depletion from solution in an actively growing culture. The heavy curve with solid points represents the exponential growth of diatoms, while the broken curve depicts the phosphate remaining in solution. Data from experiment 2W.

phate content was reduced even further. At this point the number of cells produced by a division is equal to the number that die or become dormant. But since death does not entail the immediate return of phosphate to solution, the available phosphate for uptake is only that which remains in a dissolved state. It was found experimentally that further divisions could take place even below 0.1 microgram atoms of phosphate-phosphorus per liter.

Figure 4 depicts typical relationships between the dissolved phosphate concentration and the phosphate fixed per diatom in a single experimental series. The phosphate content per diatom is observed to vary nearly linearly with the phosphate in the surrounding medium. We may thus write that

$$P_d = A + BP_s, \tag{3}$$

where A and B are constants. A would then be related to the minimal phosphate concentration per diatom, while B would be a function of the initial phosphate concentration for any given experiment. It should be noted that all points plotted in Figure 3 were taken while the diatoms were on the exponential growth curve.

To check the accuracy of the minimal phosphate content per diatom as determined radiochemically, diatoms were grown in the nutrient medium with no added phosphate. The diatoms were assayed daily for population density. At the

TABLE III

Culture flask	Final cell population, diatoms/ml.	P_d, micro-gram-atoms/diatom $\times 10^8$
1	25,000	4.3
2	22,000	6.6
3	28,000	5.1
4	28,000	3.1
5	25,000	4.9
6	25,000	5.7

approach of the leveling-off period, the diatoms were filtered onto a Whatman No. 42 7-centimeter filter paper disc. The total phosphate content of the diatoms contained in the known volume of the culture flask was determined by digesting the filter paper in 5 ml. of a 2:2:1 nitric: perchloric: sulfuric acid solution until fumes of sulfuric acid appeared. The residue was diluted to 100 ml. and an aliquot assayed for inorganic phosphate. Blank filter paper was simultaneously treated to determine the correction factor due to phosphate contained in the filter paper and the reagents. The corrected results of P_d obtained by this procedure are listed in Table III. It is manifest that they may be compared favorably with the minimal values obtained by the radiochemical method. The initial phosphate concentration was 1.1 microgram atoms of phosphate-phosphorus per liter, indicating that essentially all of the phosphate was utilized in diatom production.

One series of experiments was conducted on phosphate regeneration. The di-

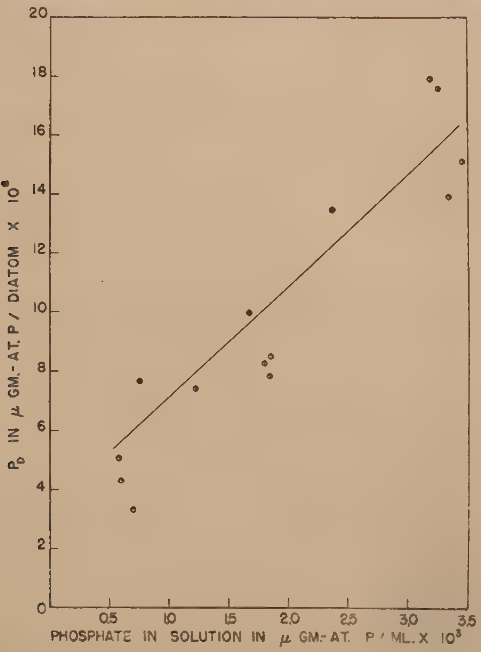

FIGURE 4. The phosphate fixed per diatom versus the phosphate concentration of the surrounding solution. Data from experimental run T.

atoms after reaching maximum growth were placed in a darkened box at 17° ± 2° C. with no stirring. Daily aliquots were taken and the supernatant liquid analyzed. As is shown in Figure 5, very little of the phosphate returned to solution after three weeks. This experiment was initiated at a low phosphate level. It would thus appear that the minimal phosphate is strongly bound. Although we may treat this experiment as somewhat of a laboratory phenomenon where the breakdown of the diatom is a function of the bacteria present, it nevertheless indicates the stable character of the bound phosphate. Further, in dynamic considerations considerably more time for death and decay of diatoms must be allowed for the return of phosphate to solution.

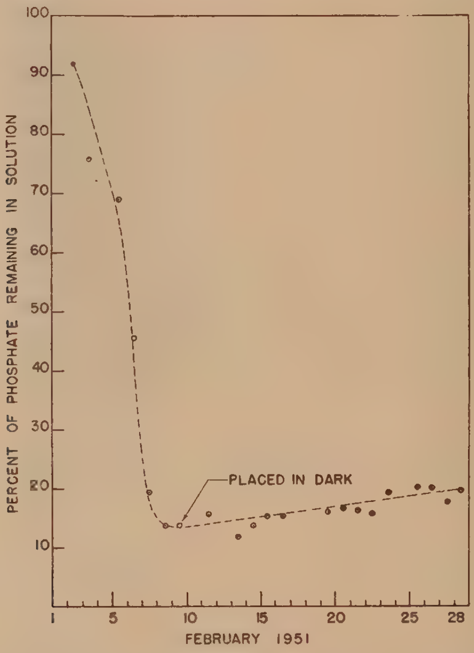

FIGURE 5. The regeneration of phosphate to the solution by diatoms deprived of light. The rapid uptake from February 2 to February 9 represents the diatom growth. Data from experiment 2Q.

In some initial experiments involving diatoms containing more than the minimal amount of phosphate, the phosphate per diatom was determined by collecting a known number of organisms on filter paper, and subsequently assaying radiochemically under the Geiger-Muller tube. However, in this process, it was found that washing the diatoms with radiophosphate-free sea water, to free them of any adhering phosphate in the nutrient medium, removed as much as 50 per cent of the phosphate from the diatoms. Thus a significant fraction of the phosphate above the minimal amount appears to be loosely bound and readily exchangeable, and we may designate it as the labile phosphate.

Discussion

From this dynamic study of the assimilation of phosphate by the marine diatom *Asterionella japonica,* it is evident that these plants have a phosphate content dependent upon that of the environment. This phenomenon, not heretofore fully established, adequately explains the anomalies in phosphate content of diatoms in both cultural and natural populations. Lund's experiments on the fresh water species *Asterionella formosa* first suggested this relationship which he designated as phosphate storage. He found that cells grown in stock culture of 74 microgram-atoms of phosphate-phosphorus per liter contained 3.7×10^{-8} microgram atoms of phosphate-phosphorus per diatom, whereas the cells in stock cultures of only 19 microgram-atoms of phosphate-phosphorus per liter contained but 1.5×10^{-8} microgram-atoms of phosphate-phosphorus each.

By these radiochemical techniques the minimum phosphate content of a diatom can be ascertained, which in the case of the species studied was about 5×10^{-8} microgram-atoms of phosphate-phosphorus per cell. This phosphate may best be designated as "bound phosphate" or the phosphate which is not readily exchangeable with that of the surroundings. Such a condition as this must obtain whenever the phosphate is incorporated irreversibly into the protoplasm. The labile or readily exchangeable phosphate should in no sense be considered as storage since this phosphate level reflects the environmental phosphate through the uptake process.

Inasmuch as this single species was able to flourish in phosphate concentrations lower than the minimum levels found in the euphotic zone of the Pacific Ocean and in surface sea water to which no phosphate had been added, it appears that the inorganic phosphate content of marine waters is representative only of the total potential population that it could support, assuming no diffusion of this nutrient. From the data in Table II of the culture experiments it can be seen that there is a limiting growth factor other than phosphate or nitrate. Moreover, sea water media enriched a second time with all nutrients or with all nutrients but phosphate and nitrate failed to produce growth of diatoms. Using this same technique on other essential elements, the authors hope to establish further minimum mineral requirements of this diatom.

The relationship between phosphate uptake and the concentration of nitrate can be qualitatively seen from the experimental data. The initial nitrate concentration in all experiments was constant at an excess of 2000 microgram-atoms per liter. From Figure 4 we see that initially the phosphate per diatom is about 16×10^{-8} microgram-atoms phosphate-phosphorus per cell, where the phosphate in solution is 3.5 microgram-atoms phosphate-phosphorus/liter. From Table II, experiment 3T, we find that at a final phosphate concentration of 4.2 microgram-atoms phosphate-phosphorus/liter, the cell content is about 5×10^{-8} microgram-atoms of phosphate-phosphorus. Thus, a high nitrate/phosphate ratio is reflected in a high phosphate content of the diatom cells. This result is in agreement with the work of Ketchum (1939).

In the present study it was not considered essential or possible to have bacteria-free diatoms. First of all, only the exponential growth phase of diatom populations was studied. Accordingly, the biomass consisted almost entirely of actively growing plants. There was thus no substrate for bacterial growth. The remarkably close correspondence between the curves of phosphate depletion and diatom growth would only result if the phosphate was entirely assimilated by the diatoms. The culture medium was autoclaved to remove any other competing living forms.

The diatom stock cultures which were used for inoculation were never freed of bacteria, inasmuch as they were healthy and normal cells. It seemed unlikely that any number of repeated washings could free these cells from bacteria which were attached between the frustule and the cell wall. Observations on decaying diatoms showed that the decay takes place within the frustule and the frustule does not open until the decay process is nearly complete. The standard procedure for determining sterility in diatom cultures is normally carried out on cells which have been repeatedly washed and never on aged cultures. It would seem that the only test for sterility should be one of direct observation as to whether the moribund cells decay.

SUMMARY

1. Studies were made on the uptake of phosphorus by the marine diatom *Asterionella japonica,* utilizing radioactive phosphorus as a tracer.

2. The higher phosphate concentrations in the solution were linearly related to higher contents of phosphate in the diatom cells.

3. A minimal cell concentration of phosphate for further growth was established for this species.

4. Two types of phosphate were found in the cells: the minimal content which was strongly bound and not removed by water washing of the diatoms and a labile phosphate which could be removed. Experiments on the release of phosphate conducted on diatoms containing only minimal amounts of it, indicated that only a small percentage of the phosphate was returned to solution as soluble phosphate after three weeks.

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Reprinted from the AMERICAN JOURNAL OF BOTANY, Vol. 38, No. 9, 669-677, November, 1951
Printed in U. S. A.

CULTURE OF THE DINOFLAGELLATE GYMNODINIUM WITH SOIL EXTRACT[1]

Beatrice Marcy Sweeney

NE OF THE MOST striking features of phyto-
nkton populations in the sea is fluctuation both
the type and in the number of cells present.
dy of plankton hauls has revealed a seasonal
vering of diatoms, and the factors promoting
r growth have long been objects of study (Har-
, 1939; Gran, 1930; Riley, 1947). The number
species of dinoflagellates also vary enormously,
ough these fluctuations are perhaps less perfect-
orrelated with time of year than in the case of
diatoms. The physiological factors which lead
apid multiplication of dinoflagellates are poorly
erstood. The purpose of this investigation was
determine what chemical factors are necessary
rapid growth of these organisms in culture.

t is known that the multiplication of certain
er plankton organisms in culture is much accel-
ted by the addition of soil extract to the culture
dium. Such extracts were first used extensively
culture media for algae by Pringsheim (1912).
ce that time, soil extracts have been widely suc-
sful in promoting the culture of organisms that
difficult to grow in inorganic media (diatoms,
vey 1939; flagellates, Lwoff and Lederer, 1935).
active principle in soil extract has not been
ntified with respect to any of these organisms.
wever, Pringsheim (1936), on the basis of ex-
iments employing *Chlorogonium*, *Polytoma*,
ytomella, and *Chilomonas* as test organisms, has
cluded that the active principle is an acid- and
aline-stable organic substance, insoluble in alco-
and ether, adsorbed by charcoal, and destroyed
hydrogen peroxide. Whatever the nature of this
nciple, it is evidently important in the nutrition
a fairly wide range of unicellular organisms.
s it seemed profitable to begin this investigation
h a detailed study of the effect of soil extract on
rate of growth of dinoflagellates.

ISTORY OF THE CULTURE OF MARINE DINO-
GELLATES.—The literature contains few records
marine dinoflagellates which have been main-
ned in culture for many transfers. A number of
cies have been cultured for short times by tax-
mists who wished to identify the organisms or
ow their life cycles. These cultures were usual-
not bacteria-free and were sometimes mixtures of
eral species, and no attempt was made to deter-
e optimum conditions for growth. Küster
08) grew *Gyrodinium fucorum* for a period of 6 months in sea water. Allen, in Plymouth, England, was probably the first to obtain a flourishing culture of a holophytic marine dinoflagellate, *Peridinium triqueta* (Lebour, 1925) and he also succeeded in growing the holozoic form *Oxyrrhis marina* in mixed culture with *Nitzschia.*

Griessman (1913) made some attempt to study the conditions which favored rapid growth of the colorless peridinian *Glenodinium cohnii.* He found it impossible to obtain bacteria-free cultures by repeated washing, because all cells encysted after several divisions and did not excyst. If no attempt was made to remove bacteria, actively-dividing cultures could be maintained in the following medium: 3.5 per cent *Fucus* extract, 1.5 per cent raw sugar, 0.15 per cent starch, 0.05–0.01 per cent tartaric acid in sea water. The addition of NH_4NO_3, KNO_3, asparagine, or peptone as sources of nitrogen had no measurable effect. Growth was possible at temperatures from 0–26°C. with the optimum in the middle of this range.

Bachrach and Lefevre (1931) failed to obtain successful cultures of the dinoflagellates *Amphidinium* on sea water agar plates and *Gymnodinium* in a liquid medium containing *Fucus* extract.

In a paper chiefly devoted to the culture of diatoms, Gross (1937) describes his attempts to grow several dinoflagellates in Føyn's "Erdschreiber" (Schreiber, 1927) which has the following composition: $NaNO_3$, 0.1g.; Na_2HPO_4, 0.02g.; soil extract, 50 cc. in 1000 cc. "outside" boiled sea water. Organisms were picked out from net samples with a small pipette and washed several times in 1-2 cc. sterile sea water. However, these cultures were not bacteria-free. His method was successful with *Prorocentrum micans*, but other dinoflagellates (*Ceratium tripos, C. fusus, C. furca, Dinophysis tripos*) failed to divide more than a few times.

In 1945, Braarud described three species of dinoflagellates, *Porella perforata*, *Gonyaulax Tamarensis* (two clones) and *Prorocentrum reticulatum*, which were grown for several months in "regular Allen culture," presumably Miquel solution without soil extract, although full details of culture technique are lacking and the purpose of the study was purely taxonomic.

In a short note, King (1950) reports that she is able to grow bacteria-free cultures of *Gymnodinium simplex* in a synthetic medium containing mineral nutrients, including those of Hoagland's A-Z solution and twelve amino acids in concentrations ranging from 0.20–0.05 g./l. These amino acids replaced yeast extract previously successful as a supplement. No growth of this *Gymnodinium* was ob-

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Received for publication January 12, 1951.
ontribution from the Scripps Institution of Oceanogra-
, New Series No. 548.
he author wishes to express her appreciation to Dr.
rston C. Sargent for his many helpful suggestions.

tained in purely mineral nutrient. Full details of her technique were not given.

Barker (1935) was the first investigator to study the physiology of dinoflagellate cultures extensively. He was able to maintain cultures of the autotrophic dinoflagellates *Prorocentrum micans*, *P. gracile*, an *Exuviella*, a *Peridinium*, a *Gonyaulax*, and a *Ceratium*, as well as a holozoic form *Oxyrrhis marina* (in mixed culture with *Nitschia*) for more than a year, and to study the effect on these cultures of temperature, light, *p*H, and the concentration of mineral nutrients. He also made measurements of their photosynthesis and respiration.

Since Barker was so successful in culturing dinoflagellates, whereas other investigators had reported considerable difficulty (Gross, 1937), it seems worthwhile to review his method in more detail here. Organisms were isolated from net samples using sterile micropipettes, washed in sterile medium two or three times if species-pure cultures were desired, or five or six times for bacteria-free cultures. Such bacteria-free cultures were obtained of *Prorocentrum micans*, *P. gracile*, and the *Peridinium* only, and these forms were used in the physiological studies. All stock cultures were grown in the following nutrient medium made up in aged sea water: KNO_3, 0.01 per cent; K_2HPO_4, 0.001 per cent; $FeCl_3$, 0.00001 per cent; soil extract, 2 per cent. The optimum temperature lay between 18°–20°C. and the cultures were kept at 18±0.1°C. in a thermostatically controlled water bath. The optimum *p*H lay between 8–9, that of the sea water media used. Cultures were supplied with constant illumination of 2000 erg/mm.^{2}/sec. (or 75000 M.C.). Pyrex test tubes containing 3 ml. liquid medium were used as culture vessels.

Under these conditions, growth of the dinoflagellates continued for 10 days at an undiminished rate, and populations reached 10,000 cells per ml. Barker found that nitrate and phosphate could be omitted from the culture medium without affecting the rate of growth, and concluded that the limiting concentrations of these nutrients must lie below that already present in the sea water used to make up media, that is, for nitrogen, at a concentration of 0.01–0.001 p.p.m. Ammonium ion proved to be poisonous to these organisms at concentrations above 1 p.p.m. Sometimes growth was obtained in the absence of soil extract, but this was erratic. Soil extract could not be replaced by inorganic or organic iron, or Hoagland's A-Z solution of minor elements. No effect of *Fucus* extract, yeast autolysate, glucose, or sodium acetate could be demonstrated in species-pure cultures. The following organic substances in sterile 0.1 per cent or 0.01 per cent solution in mineral nutrient in the light failed to show more growth than the standard nutrient medium containing soil extract: peptone, asparagine, glycine, leucine, mannitol, sodium acetate, potassium butyrate, calcium lactate. No growth took place in any of these media in t
dark.

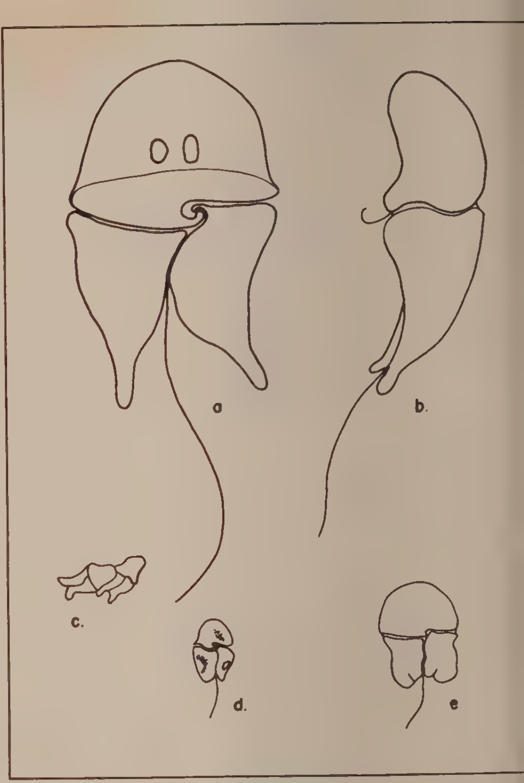


Fig. 1. *Gymnodinium splendens* drawn from hanging dr
live preparation. a, Ventral view showing girdle, sulc
nucleus just divided, and longitudinal flagellum; b, si
view; c, two recently divided cells still attached; d, sm
type cell grown in mineral nutrient, without suppleme
showing dark granular inclusions; e, round form. a,
×625; c, d, e ×190.

METHOD.—*Organism.*—For the purpose of th
study, a *Gymnodinium* which occurs in La Jo
waters in the winter was used. It was first isolat
from a net sample December 28, 1948, and t
strain from which a single clone was finally mai
tained in subculture was isolated on January 1
1949. This clone is still growing vigorously
subculture at the present time (May, 1950).

The following characteristics place this orga
ism in the genus *Gymnodinium* (fig. 1): two f
gella, transverse girdle and longitudinal sulcus,
exoskeleton of discrete plates, no tentacle or oc
lus, no torsion of the body, girdle making not ov
one turn, girdle displacement not over 0.2 of
total length. It was not possible to identify t
species with certainty since its characteristics do n
conform precisely to any species of which a descri
tion could be found (Kofoid and Swezy, 1921; I
bour, 1925; Kofoid, 1931). However, consideri
the known variability of species of dinoflagellat

raarud, 1945) and the relative insignificance of e differences between this organism and *G. splen- ns* Lebour, its description as a new species did t seem warranted.

The *Gymnodinium* here studied (fig. 1, a, b) is oval cell flattened dorsiventrally, reniform in oss-section, with about equal epicone and hypo- ne. The girdle is slightly impressed, displaced out a girdle width and the anterior flagellar pore at the junction of the sulcus and the girdle. The lcus does not extend into the epicone but expands steriorly to *deeply* notch the antapex. The de- ee of notching of the antapex varies widely with e physiological condition of the cell, being con- lerably more marked in the actively growing con- tion than in *G. splendens* figured by Lebour. The ngitudinal flagellum is longer than the body and rected backward, propelling the organism by a hiplike motion. The transverse flagellum nearly circles the girdle and lies in it. The nucleus is bcentral and slightly anterior. The color of this ganism is brown, rather than yellow as described r *G. splendens* by Lebour, and no definite ar- ngement of chromatophores, which are small ther than large and elongated, could be observed. some cases, the epicone center appears clear, but individuals from actively growing cultures, this s not the case. Fission is longitudinal oblique g. 1, c). This description fits *G. splendens* with e exceptions noted. In the single clone studied, ere is a marked variation in size, shape, and loring, depending on physiological conditions. e usual size is 80μ long, 46μ wide, 34μ thick, hough in cultures dividing in mineral nutrient uch smaller individuals may be encountered, *i.e.*, μ long (fig. 1, d). These cells may be very pale n in color or almost colorless, and sometimes ow dark granular inclusions. According to Le- ur *G. splendens* is somewhat smaller (54–56μ ng). Rounded forms are often encountered in ltures under unfavorable conditions when no vision is taking place.

Isolation of cells.—The standard procedure for tting up a culture experiment was as follows: iginally *Gymnodinium* cells were picked up with sterile micropipette from net samples and subse- ently from flourishing cultures usually about 4 eeks old. These cells were then washed three nes in 5 ml. sterile sea water or mineral nutrient lution. From the third washing dish, *five* cells ere placed in each culture vessel. The resulting ltures were free from any visible contaminant, hough small numbers of bacteria were undoubt- ly present.

Some further attempt was made to obtain bac- ria-free cultures by washing cells five to six times stead of three times in a lucite transfer chamber eviously sprayed with 70 per cent alcohol. The chnique of transferring a single cell through suc- ssive drops of sterile nutrient solution was not practical with this organism, since the evaporation from a drop of sea water was rapid enough to change the salinity and cause disintegration of the cell. The sterility of the resulting cultures was tested by transferring cells to nutrient solution containing 0.2 per cent peptone and dextrose, a medium favoring the growth of bacteria and molds. The solution in such cultures remained clear for 5-10 days. Such sterile cultures behaved in no way differently from cultures which were not tested for sterility, so that it may be assumed that the few bacteria possibly present in the latter did not play an important physiological role in the growth of such cultures.

Culture vessels.—The culture vessels were soft glass watch glasses of about 10 ml. capacity. Before use, these dishes were always washed in boiling 2 per cent HNO_3, then in boiling distilled water, and were then soaked overnight in "standard" sea water. After washing, they were wiped dry with a clean towel and autoclaved dry inside deep Petri plates. Similar dishes were used for washing the cells. Micropipettes were washed in the same way. All glassware was sterilized before use.

Sea water.—The sea water used for making up all media was collected from the ocean in an area off shore of very low phytoplankton population on either November 4, 1948 or March 14, 1949, and aged in the laboratory in the dark for at least 2 months before use ("standard" sea water). The purpose of aging the sea water was to remove traces of organic matter through bacterial action. The mineral nutrient solution contained the following concentration of salts per liter of the "standard" sea water described above: KNO_3, 2×10^{-3}M; K_2HPO_4, 2×10^{-4}M; $FeCl_3$, 6×10^{-6}M; $MnCl_2$, 6×10^{-7}M. This mixture was autoclaved and allowed to stand at least 2 weeks before use.

Supplementary extracts.—Soil extract was made up in water redistilled from an all-glass still, 100 g. soil (from the Scripps garden unless otherwise stated) in 100 ml. water. This mixture was autoclaved, allowed to stand overnight, decanted, and the clear solution thus obtained reautoclaved.

The yeast suspension was prepared from Brewer's Yeast Harris: to 100 ml. (6 g.) yeast powder was added a mixture of 8 ml. 95 per cent ethanol, 1 ml. conc. H_2SO_4, 6 ml. diethyl ether. A 1 per cent suspension was then made up in redistilled water and autoclaved. A simple 1 per cent suspension of yeast powder in water was also prepared. No difference was noted in the effect of these two extracts.

The *Prorocentrum* plasmoptysate was prepared as follows: 10 ml. cultures of *Prorocentrum micans* in mineral nutrient solution and 4 per cent soil extract, containing about 6000 cells per ml., were filtered through a sterile sintered glass filter of medium pore size. The filtrate was discarded, and to the cells on the filter was added 10 ml. redistilled water. This mixture was allowed to stand 15 min-

TABLE 1. *Growth of Gymnodinium in various culture media.*

Culture medium	Number of cultures	Average number of divisions per day	Average final population
Autoclaved "standard" sea water	10	0	
Mineral nutrient	56	0	
	40	0.350	9600
Mineral nutrient + 4% soil extract (active)	27	0.422	51500
Mineral nutrient + A_4 and B_7	3	0.275	123
Mineral nutrient + Fe citrate (5 mg./l.)	3	0	
Mineral nutrient + alanine (5 mg./l.)	3	0.13	21
Mineral nutrient + l-cystine (5 mg./l.)	3	0	
Mineral nutrient + asparagine (5 mg./l.)	3	0	
Mineral nutrient + vitamins (10 mg./l.)	2	0	
Mineral nutrient + peptone-dextrose, 0.2%	7	0	
Mineral nutrient + bean extract, 4%	4	0	
Mineral nutrient + yeast extract			
4%	3	0	
0.4%	2	0	
0.01%	2	0	
Mineral nutrient + amino acids (King, 1950)	5	0	
Mineral nutrient + *Prorocentrum* plasmoptysate, 4%	10	0.424	16960

utes until the *Prorocentrum* cells were plasmolysed. Suction was then applied, and the filtrate so obtained was the plasmoptysate. This was not autoclaved unless so stated. This procedure was adapted from the method of Garnjobst, Tatum and Taylor (1943) for making plasmoptysate of marine *Pseudomonas* containing accessory growth factors for *Colpoda duodenaria.*

Physical conditions.—All cultures were maintained in a controlled temperature room at 16 ± 2°C. Since these organisms did not grow without light, constant light was provided by a bank of four fluorescent "daylight" tubes 54 cm. above the cultures. The intensity at the level of the cultures as measured with a GE photometer was 60–70 foot-candles. A further control of temperature fluctuation and humidity was provided by placing distilled water inside each Petri plate around the culture dish.

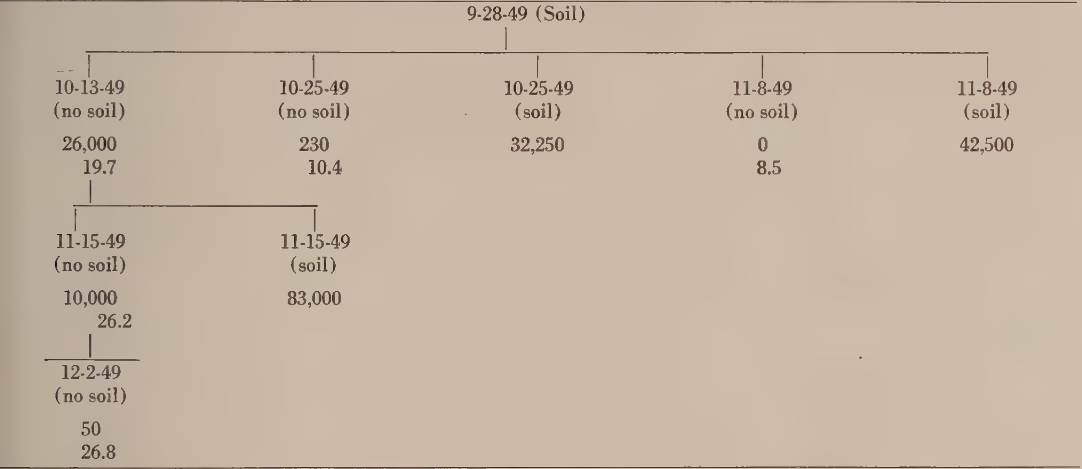
Recording.—Growth of the cultures was determined by counting the entire population present in a given culture vessel under a dissecting microscope with the aid of a grid ruled on the under surface of the culture dishes with a diamond pencil. When the population became too large to make this method of counting feasible, aliquots were removed with sterile graduated pipettes. The number of cells present in each culture was plotted against time on semi-log graph paper, and the rate of growth, expressed as the number of divisions per day, was obtained from the straight line portion of the graph. Counts of cultures were made until such time as two successive counts showed no increase in population. The maximum number of cells was thus recorded for each culture. Counting the entire population of each culture avoided sampling errors.

Stock cultures were maintained under the con
tions described above in mineral-enriched "star
ard" sea water with 4 per cent soil extract.

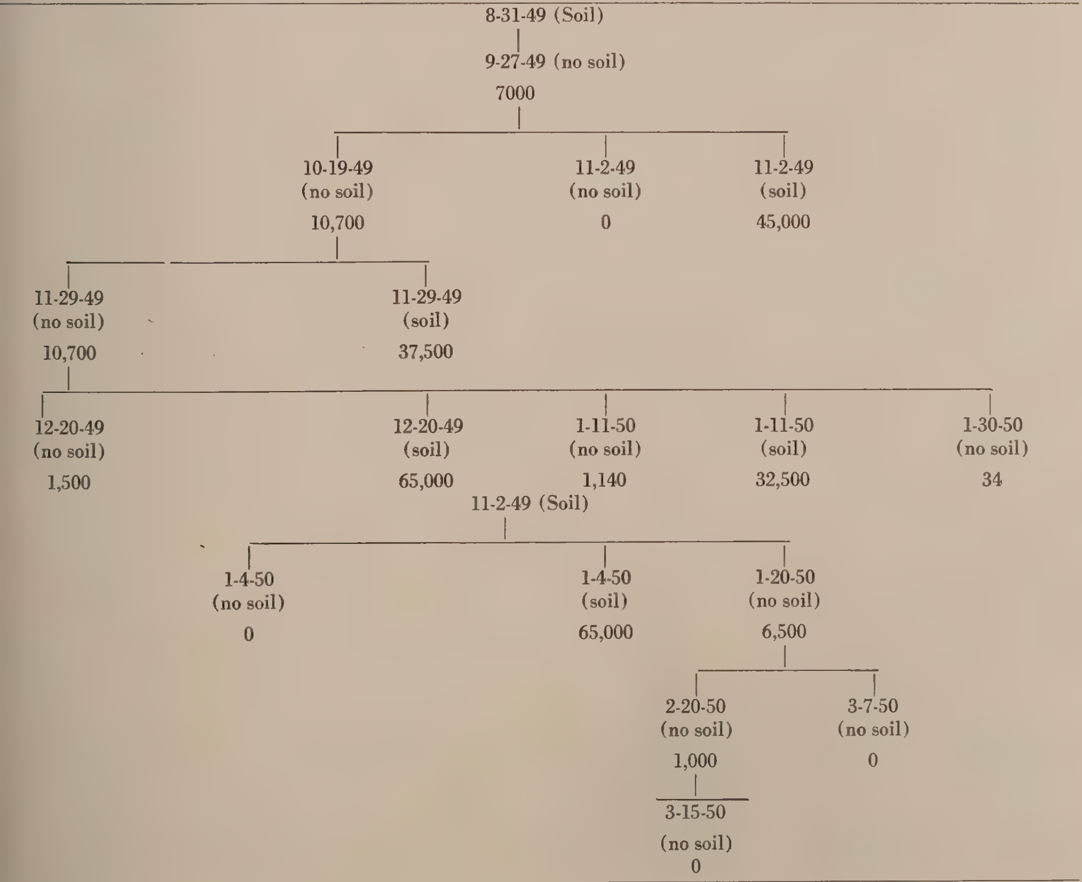
RESULTS.—When cells of *Gymnodinium sple*
dens were placed in autoclaved, aged sea wa
(standard sea water) without supplementary f
tors, mineral or otherwise, no division took pla
in any of ten cultures (table 1). It may be
sumed, therefore, that this water, after autoclavi
does not contain certain substances necessary
the growth of this organism.

The possibility that the missing factors were m
eral nutrients was first examined. When nitrog
phosphorous, iron, and manganese were added
the standard sea water, *Gymnodinium* either did
divide at all, or growth was poor or erratic (ta
1). When repeated subcultures in this miner
enriched medium were made using as innocula
cultures which had shown the best growth in m
eral nutrient solution, then it was found that
final populations reached became smaller in ea
subculture, until, in the third or fourth subcultu
no growth was obtained (tables 2 and 3). The
servation that *Gymnodinium* could not be subc
tured indefinitely in mineral nutrient solution s
gests that this medium lacks some substance or s
stances necessary for the growth of this organis
When this factor, accumulated within the cells
excess previous to their transfer into mineral
trient solution, became exhausted, then the c
ceased to divide. The total number of divisions
each cell, originally taken from the stock cult
containing soil extract, may be estimated (table
From this table, it may be seen that the new mine
nutrient solution supplied in the third subcult
did not increase the number of divisions, and ab
twenty-six divisions have taken place in this p

ABLE 2.—*Final population and total number of cell divisions in serial subcultures of Gymnodinium in mineral nutrient with and without soil extract. For each culture, the top line shows the date of inoculation, and the lines below show respectively the final population and the total number of cell divisions since 9-28-49.*


9-28-49 (Soil)
10-13-49
(no soil)
26,000
19.7
10-25-49
(no soil)
230
10.4
10-25-49
(soil)
32,250
11-8-49
(no soil)
0
8.5
11-8-49
(soil)
42,500
11-15-49
(no soil)
10,000
26.2
11-15-49
(soil)
83,000
12-2-49
(no soil)
50
26.8

ABLE 3.—*Final population in serial subcultures of Gymnodinium in mineral nutrient with and without soil extract. For each culture, the top line shows the date on inoculation, and the line below shows the final population.*


8-31-49 (Soil)
9-27-49 (no soil)
7000
10-19-49
(no soil)
10,700
11-2-49
(no soil)
0
11-2-49
(soil)
45,000
11-29-49
(no soil)
10,700
11-29-49
(soil)
37,500
12-20-49
(no soil)
1,500
12-20-49
(soil)
65,000
1-11-50
(no soil)
1,140
1-11-50
(soil)
32,500
1-30-50
(no soil)
34
11-2-49 (Soil)
1-4-50
(no soil)
0
1-4-50
(soil)
65,000
1-20-50
(no soil)
6,500
2-20-50
(no soil)
1,000
3-7-50
(no soil)
0
3-15-50
(no soil)
0

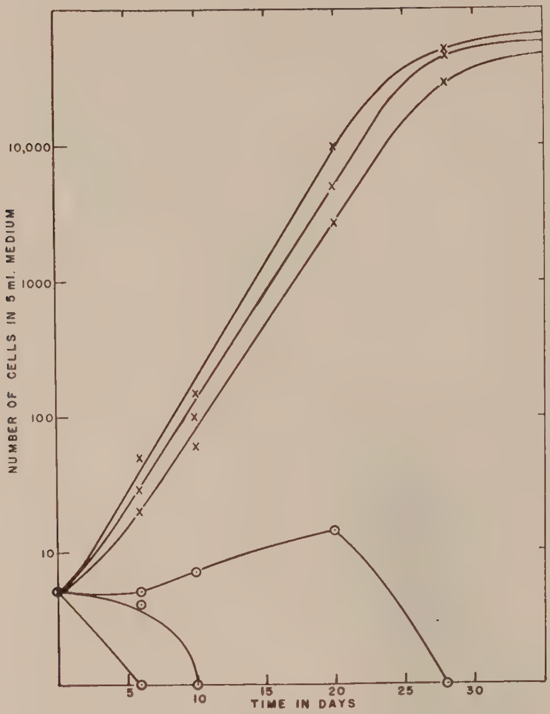


Fig. 2. Rate of growth of *Gymnodinium* in soil extract; experiment started 11-8-49. (x) Mineral nutrient containing 4 per cent soil extract prepared 10-11-49. (o) Mineral nutrient without soil extract. Each point represents the number of cells in a single culture.

ticular instance before the supply of the missing factor was exhausted.

Since iron in inorganic form may not always be available for plant growth, organic iron as ferric citrate (5 mg./l.) was added to cultures of *Gymnodonium* in the basic mineral nutrient solution described above. Sodium citrate was added to the control cultures. No effect on growth by either ferric citrate ion complex or citrate ion could be observed (table 1).

In addition to the mineral nutrients, nitrogen, phosphorous, iron and manganese, other mineral ions which have been found to be essential or beneficial to the growth of higher plants were tested to see whether they might supply the missing factor for the growth of *Gymnodinium*. The solutions were Hoagland and Arnon's (Arnon, 1938) so-called minor mineral nutrients A_4: (boron, 0.5 p.p.m.; manganese, 0.5 p.p.m.; zinc, 0.05 p.p.m.; and copper, 0.02 p.p.m.) and B_7 (molybdenum, vanadium, chromium, nickel and cobalt, 0.01 p.p.m.). Tungsten and titanium were omitted because these were not available. When these elements were added to the mineral-enriched sea-water containing nitrogen, phosphorous, iron and manganese, no increase in the rate of growth or the
final population was observed (table 1). In six o
of nine experiments, no division took place wi
or without minor element ions. Neither A_4, nor B
nor both together, supplied the missing factor
factors on which the growth of *Gymnodinium* d
pends. It seems likely that these factors are n
mineral in nature.

When soil extract was added to cultures of *Gy*
nodinium growing in mineral-enriched sea water,
was possible to subculture these organisms inde
nitely (the present strain has at the time of writi
been maintained in culture in 4 per cent soil e
tract for a period of 15 months and is in good co
dition). Cultures supplied with soil extract rea
high populations of 10-20,000 cells per ml. a
the growth rate lies between 0.4 and 0.5 divisio
per day under the conditions used (fig. 2).
mentioned above, stock cultures were maintained
4 per cent soil extract.

An interesting situation exists in regard to t
activity of soil extract. When first prepared,
extract showed growth-promoting activity. Aft
the extract had stood at 16°C. for 4-6 weeks, it d
veloped full activity. Activity persisted for perio
of from 4 to 6 weeks and then disappeared (fig. 3
This course of events was followed for six differe
extracts of garden soil with only slightly varyi
time relationships. Activity was developed wheth
or not tubes containing the extract were open
during the 4-6 week period of storage. Since e
tracts were reautoclaved following decanting a

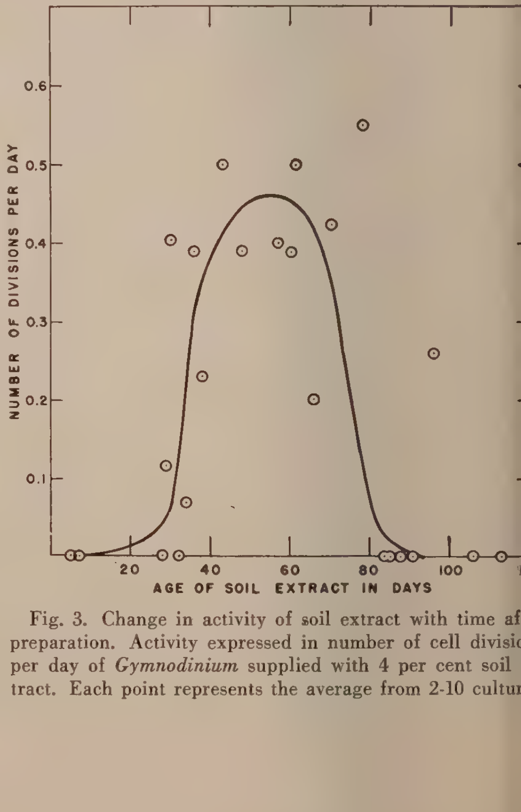


Fig. 3. Change in activity of soil extract with time af
preparation. Activity expressed in number of cell divisi
per day of *Gymnodinium* supplied with 4 per cent soil
tract. Each point represents the average from 2-10 cultu

ere kept in tubes which were carefully plugged
id covered, and since no cloudiness could be ob-
rved in the extract, it seems improbable that
icrobial contamination played any part in the
evelopment of activity. A gradual chemical change
ust take place in the sterile extract, which alters
s composition so that at the end of the ripening
eriod of about 4 weeks, it shows growth-promot-
g activity. As this chemical process proceeds,
e extract again loses activity. It is not possible at
e present time, to delineate this change with cer-
inty. The simplest explanation for this behavior
that soil extract contains a substance which is
vorable to the growth of *Gymnodinium* at medi-
n concentrations but unfavorable at high con-
ntrations. It is possible that the concentration
this substance is either increasing or decreasing
ntinuously with time of storage. Both these pos-
bilities were considered, first that the concentra-
on of the active substances was increasing with
ne. If this were the case, then dilutions of ex-
acts which no longer showed activity at 4 per
nt should show activity at some lower concen-
ation. This did not prove to be the case, since
il extracts so old that activity at 4 per cent was
st were also inactive at 0.4 per cent, 0.04 per cent
id 0.004 per cent. Next let us consider the possi-
lity that the concentration of growth-promoting
bstance decreases continuously with time of stor-
e of the soil extract. If this were the case, then
me concentration of freshly prepared soil extract
naller than 4 per cent should show activity. How-
er, freshly prepared soil extract was inactive at
4 per cent, 0.04 per cent, 0.01 per cent, 0.0001
r cent and 0.000001 per cent, and showed defi-
te toxicity in some experiments at 0.4 per cent
id 0.01 per cent.

However, extracts about 3 weeks old, which were
ot yet active at 4 per cent, in one experiment
owed activity at 0.4 per cent. This suggests that
e concentration of the active substance in soil
tract decreases with time, and that this accounts
r the loss of activity in old extracts (8–10 weeks).
ne inactivity of freshly prepared extracts cannot
explained on this basis alone, however, as shown
ove. It may be that toxic substances as well as a
owth-promoting factor are present in soil extract
ien freshly prepared, and that these disappear
iring aging of the extract. The shape of the
rve (fig. 3) certainly suggests that it could be a
mposite of two curves, one ascending and one
scending. The descending curve would repre-
nt the decreasing concentration of growth-pro-
oting factor as soil extract ages. The ascending
rve may represent the decrease in the negative
fect of a toxic substance also decreasing in con-
ntration with aging of the soil extract, or the in-
easing concentration of a second growth-promot-
g factor. No evidence is, as yet, at hand to de-
de this point, but further work is in progress.

The relatively short period of activity of soil extract posed a practical problem. It was desirable to discover a method of preserving active soil extracts. Reautoclaving after activity had developed did not change its activity or the rate of loss of activity. Refrigeration at about 4°C. was not effective in preserving activity. However, active extracts deep-frozen at —25°C. retained activity for a period of at least 6 months.

Since no mineral supplement was found which could support continued subcultures of *Gymnodinium*, an attempt was made to identify the active substance present in soil extract with one of the organic substances known to promote growth of other organisms. For this purpose, a mixture of vitamins was prepared which supplied the following substances to the cultures at a concentration of 10 mg./l.: indole-3-acetic acid, thiamine, uric acid, inositol, nicotinamide, pyridoxine, riboflavin, yeast nucleic acid, and vitamin C. In one case, l-cystine also was included in the mixture. These substances in this concentration and combination were not active in bringing about division in *Gymnodinium*. It is possible that the toxicity of one substance in the mixture may have masked the activity of another. Time did not permit the assay of each substance separately. Alanine, cystine, and asparagine added to cultures in mineral nutrient solution separately at a final concentration of 5 mg./l. were without effect. The mixture of amino acids which King (1950) reported to be a successful supplement to mineral nutrient medium for the growth of *Gymnodinium simplex* proved inactive for *Gymnodinium splendens* at the concentration which she employed. This mixture has the following composition: dl-arginine, 0.2 g./l.; l-histidine, 0.05 g./l.; l-leucine, 0.2 g./l.; dl-lysine monochloride, 0.2 g./l.; dl-methionine, 0.05 g./l.; dl-phenylalanine, 0.1 g./l.; dl-threonine, 0.15 g./l.; l-tryptophane, 0.05 g./l.; l-tyrosine, 0.15 g./l.; dl-valine, 0.2 g./l.; l-cystine 0.05 g./l. (isoleucine was omitted). Further work on the effect of amino acids on the growth of *Gymnodinium* is in progress. Mixtures of 0.2 per cent peptone and 0.2 per cent dextrose used for testing for possible bacterial contamination did not support any growth of *Gymnodinium*.

Since no factor of known composition, available for testing, replaced soil extract for the growth of *Gymnodinium*, several crude extracts were assayed (table 1). Yeast extract at concentrations of 4 per cent, 0.4 per cent, 0.1 per cent was inactive. Extract of green beans prepared according to Bonner and HaagenSmit (1939) and presumably containing the leaf growth hormone adenine was inactive at 4 per cent, either raw or autoclaved. Extracts of commercial "rhizobized" oak leaf-mold prepared by the same method as soil extract were inactive over a period of a month. Similar extracts of commercial steer manure showed slight activity in one experiment 6 weeks after preparation, other experiments being negative.

To date, the only other source of active principle is cells of another dinoflagellate, *Prorocentrum micans*, also grown in 4 per cent soil extract. When a plasmoptysate of *Prorocentrum* cells is prepared as described above, the resulting colorless extract is as active in promoting division of *Gymnodinium* as is soil extract (fig. 4). Freshly prepared extract is active and remains so for about 10 days at 16°C. A small amount of activity is also present in the medium in which the *Prorocentrum* cells had been growing. Living bacteria from the *Prorocentrum* culture are probably not responsible for the growth promoting property of the plasmoptysate, since peptone-dextrose plates inoculated from actively growing *Gymnodinium* cultures in 4 per cent plasmoptysate did not show the presence of either bacteria or mold contaminants. The active factor or factors apparently originate from the *Prorocentrum* cells. From the data at hand, it is not possible to determine whether the active factor or factors in the plasmoptysate is concentrated by the *Prorocentrum* cells from the soil extract supplied them, or whether the *Prorocentrum* cells contribute to the active material by synthesis. There seems no reason at present to consider the active principle in plasmoptysate different from that in soil extract.

Since the *Gymnodinium* studied here sometimes reaches large numbers in the coastal waters off La Jolla, the question arises whether this water also contains an active division-promoting substance or substances similar to that in soil extract. To investigate this point, sea water was collected at La Jolla during the height of a bloom of this organism on December 28, 1948. Cells of this *Gymnodinium* cultured in this water without supplement of any kind divided two to three times. Filtering the water removed the activity. The presence of an active substance in the water was more clearly demonstrated when this water was added to mineral nutrient solution made up in "standard" sea water at a concentration of 4 per cent (fig. 5). Inshore water collected on two subsequent days when *Gymnodinium* was not present in large numbers among the phytoplankton did not show any growth-promoting activity.

Discussion.—It seems clear that this *Gymnodinium* requires for division and growth the presence in small quantities of some factor not yet identified, but supplied by soil extract. From the experiments with various mineral nutrient solutions, it seems probable that this factor in soil extract is not mineral but organic. Such an organic substance could act in one of two different ways, either as a growth substance directly concerned in cell division, or as a chelating agent, which either made available a mineral nutrient present in the mineral nutrient solution but not absorbable as a mineral ion, or reduced the concentration of an ion present in the mineral nutrient solution in too high a c centration. That the active factor in soil extrac purely a chelating agent seems improbable si other mixtures of organic substances, such as ye and bean extracts, which would be expected a to supply chelating agents, are inactive. Furtl more, it would be difficult to explain the effect aging on soil extract and the carrying over of act principle from one transfer to the next on this ba Then too, citrate ion, a chelating agent, was in tive. The most likely hypothesis at present wo seem to be that soil extract contains some gro substance, although chelating agents may also p a role in the activity of soil extract.

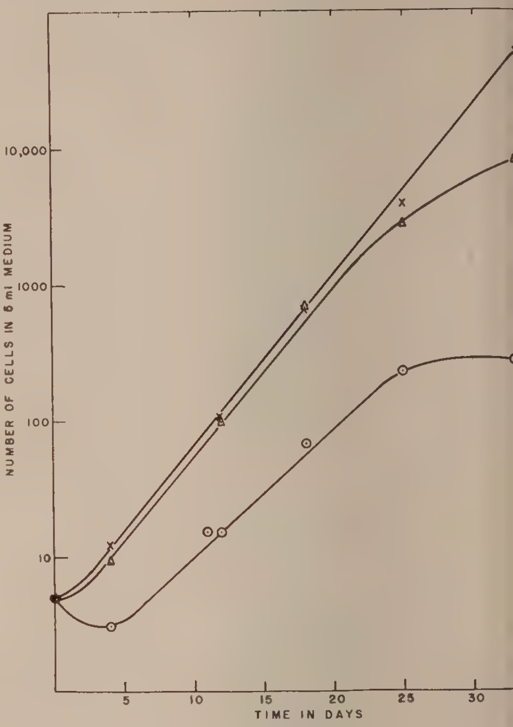
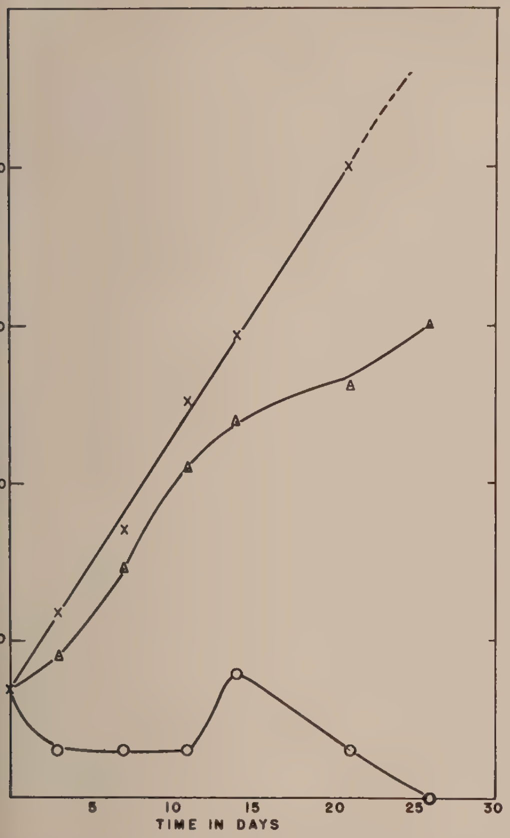


Fig. 4. Rate of growth of *Gymnodinium* in *Prorocent* plasmoptysate. Experiment started 6-2-49. (Δ) Min nutrient containing 4 per cent plasmoptysate prepared 49. (x) Mineral nutrient containing 4 per cent soil tract prepared 4-15-49. (o) Mineral nutrient without plement. Each point represents the average of three tures.

These findings agree with those reported in literature in the following respects: (1) that li or erratic growth of dinoflagellates is obtained culture in sea water mineral nutrient, and (2) the missing factor or factors may be supplied soil extract. The difficulty experienced by so workers in growing dinoflagellates in soil extr may be explained in the light of the toxicity freshly prepared soil extracts here described.



ig. 5. Rate of growth of *Gymnodinium* in raw sea er; experiment started 1-14-49. (△) Mineral nutrient taining 4 per cent raw sea water collected at La Jolla 8-48. (x) Mineral nutrient containing 4 per cent soil act prepared 10-28-48. (o) Mineral nutrient without plement. Each point represents the number of cells in culture.

ure of the active fraction in soil extract is being died further at the present time.

SUMMARY

The isolation and culture of an unarmoured dino- ;ellate, tentatively identified as *Gymnodinium* *endens* is described. This organism could not be cultured indefinitely without the presence of a tor or factors present in extracts of garden soil. l extract was not active freshly prepared, but ame active after aging for a period of 4-6 weeks a sterile condition. Extracts lost activity after a iod of 2-3 months but could be preserved by p-freezing. Activity was also present in plas- ptysate of *Prorocentrum micans* cells and in sea ter collected during a bloom of *Gymnodinium*. ric citrate, sodium citrate, Hoagland and Ar- 's minor mineral nutrients, alanine, cystine, aragine, a mixture of growth substances, peptone, dextrose, yeast extract, bean extract, and extracts of leaf mold and steer manure were all inactive at the concentrations assayed.

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BULLETIN OF THE GEOLOGICAL SOCIETY OF AMERICA
VOL. 62, PP. 1413-1418 DECEMBER 1951

SUBMARINE EROSION, A DISCUSSION OF RECENT PAPERS

BY FRANCIS P. SHEPARD

INTRODUCTION

Papers in the Bulletin by Woodford (1951), Ericson, Ewing, and Heezen (1951), and an abstract by Crowell (1950) all point to a submarine origin for submarine canyons. The papers are very thought-provoking and should cause advocates of subaerial origin of submarine canyons to give serious reconsideration to their opinions. The importance of submarine processes is indicated by the enormous quantities of sand that have been carried, persumably by turbidity currents, out of the Hudson Canyon and distributed out over the deep sea plain beyond (Ericson *et al.*, 1951). The evidence that these sand movements have continued up to recent times is equally significant. This information might have been even more impressive had it been more documented and if it had been supported by reference to the recent work of the Swedish Deep-Sea Expedition and of the Scripps Institution and Navy Electronics Laboratory which has shown the presence of sand of similar characteristics out over many other parts of the ocean floor (Arrhenius, 1950; Shepard, 1951a; and papers by F. B Phleger, J. C. Ludwick, H. W. Menard, and F. P. Shepard in a symposium presented before the Society of Economic Paleontologists and Mineralogists meeting in Chicago, April 1950).[1] The present writer has referred to the movement of sediment out along submarine canyons in numerous papers for the past 20 years although it is only recently that the evidence has shown how far seaward this material is carried and what huge quantities are involved.

Woodford's valuable paper does not contribute new information from the sea floor, but it does show the failure of a simple submergence hypothesis to account for the gradients of typical sumbarine canyons and presents evidence, as does Crowell's paper, that the upper parts of the submarine canyons have walls consisting of Pleistocene and probably post-Pleistocene material. This last point might indicate that the cutting is still in process and thus infers that the canyons are of submarine origin. (For another interpretation, *see* Shepard, 1951b.)

These papers appear to be convincing, but they all fail to discuss most of the serious objections to submarine erosion as the underlying cause of the canyons and they overlook the numerous characteristics of submarine canyons which favor an initial erosion by rivers. Insofar as the writer knows, no information has yet been produced which rules out the hypothesis that the canyons were originally cut by streams in the remote past and have since been maintained and modified by landslides and other marine processes (first suggested by Shepard, 1934; most recent revision, Shepard, 1951b). If such evidence exists, its presentation would be much appreciated by all. Advances are being made so fast in submarine geology that hypotheses should be kept in a fluid state.

CANYON CHARACTERISTICS AND SUBMARINE ORIGIN

Delta-front Depressions

In considering the type of submarine feature which might be expected to exist if the valleys of the sea floor are primarily the product of subaqueous erosion, attention should be called to the valleys which are known to exist on the fronts of deltas, particularly where those deltas have been built out onto steeply sloping sea or lake floors. These are the only sure cases of subaqueous valley formation. The valleys of the Swiss deltas are well known (*see* Woodford, 1951, Fig. 8A; Kuenen, 1950, Fig. 227), and similar features occur on the fronts of some deltas built into the ocean. These valleys are rather typical of landslide scars having broadfloored, shallow, and irregular troughs with leveelike elevations along the sides of their outer courses. In some places they have distributaries. Similar features are found along the lower shallow valley extensions of submarine canyons, but the main portions of the canyons are typical river canyons and entirely different from the delta-front depressions. The submarine-canyon characteristics will be considered individually.

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[1] Appearing in Jour. Sedim. Petrol., Bull. for October or November 1951.

Submarine-Canyon Tributaries

It is notable that delta-front valleys have few if any tributaries. Woodford states (p. 842) in reference to the California submarine canyons, "tributaries, named or unnamed, are relatively rare, though several canyons are like the Monterey in having two or three or four." This statement is seriously in error as applied to California or to any other submarine canyons in areas where there are adequate surveys. Thus Monterey Canyon has at the very least 26 tributaries, and there is little doubt that more-detailed surveys would show more tributaries, as has invariably happened where more-detailed surveys have been made elsewhere. In fact, the tributaries of the best-known submarine canyons, Scripps and Carmel, are comparable in number with tributaries in adjacent land canyons.

Relative to tributaries, students at Scripps Institution have recently been swimming with aqua-lungs along the narrow, steep ridge which separates two of the tributaries of Scripps Canyon and have discovered small steep-sided gullies cut into one side of this ridge. Since there is no surface on top of the ridge on which there could be any gathering ground for the sediment necessary for trubidity currents, erosion by this process could not account for these features.

Estuaries and Canyon Heads

The submergence of rugged land areas cut by canyons should produce deep estuaries. Woodford, however, states (p. 843) ". . . . not a single California canyon heads in an estuary." This is not quite accurate since the canyons of Carmel Bay head in short estuaries (Shepard and Emery, 1941, Fig. 27). Furthermore, many canyons in other parts of the world ent estuaries (Shepard, 1948, Figs. 74, 75, 7 79). The well-known canyon which heads de into the estuary of the Congo is most difficu to explain unless, some time in the pa subaerial erosion of a canyon occurred at th place and submarine mass movements an attendant turbidity currents along the c canyon axis have maintained the canyon po tion. Certainly the great deposition at t mouth of the Congo would have prevented t excavation of a canyon across the broad sh at this particular place.

The absence of estuaries at the heads of mo canyons is by no means surprising if the canyo were cut in the remote past and have be maintained by slides and turbidity curren (Shepard, 1951b). Presumably, ample time h existed for the straightening of the coasts a combination of waves attacking headlan and streams filling estuaries.

Deep Gorges in Hard Rock

Some of the advocates of submarine erosi have considered that a few deep canyons c in firm rock are subaerial in origin, and y there is ample evidence that representati canyons the world over are cut into rock, so of it being known to consist of granite a other hard crystalline types. An examination the evidence shows that it is virtually i possible to separate these rock-walled canyo from those cut in alluvium or other soft m terial (Shepard, 1948, p. 209–229). If we co sider how canyons might develop under wat by landslides and by their attendant turbidi currents (no other process appears to be capal of producing these currents), we can reasonab start with a slope having a mantle of sedimen Let us assume that slides occur on this slop and valleys like those of the delta fronts resu Since the exploration of submarine canyo has shown that rock commonly lies at relative slight depths below this sedimentary mant it can further be assumed that the sliding a the production of sediment for turbidity cu rents would continue until the underlying ro was exposed. The rock on this new surfa would obviously be much less likely to sli than the overlying sediment. As a result, slid on other portions of the slope would become relatively more important so that eventually there would be a rock surface with little or no sediment to allow canyon cutting into the underlying rock. No such slopes have been discovered which suggests that deposition on the slopes is, in general, keeping pace or exceeding slumping. Therefore, it seems likely that the canyons were cut by a process such as stream erosion where the water would tend to concentrate along the initial depressions.

Canyons Related to Large Land Rivers

Woodford (p. 843) refers to the "... failure of sea and land valleys to join." If the canyons had been submerged recently, one could expect a close connection between most of the land and sea valleys. If the canyons were sumberged in the remote past, however, there would be no particular reason why present-day rivers should enter the sea directly opposite submarine canyon heads. Actually many of the large rivers have large submarine canyon continuations, as for example the Congo, the Columbia, the Mississippi, the Niger, and the Indus. It is particularly significant that the canyon off the Mississippi appears to have a buried extension, determined by geophysical prospecting, which connects with the abandoned and deeply submerged Pleistocene channel of the Mississippi (Fisk, 1944). The relation of all the main valleys of southern Washington —the Columbia, Willapa, Chehalis, and Quinault rivers—with adjacent submarine canyons can be no coincidence.

The relation of the large river mouths to large submarine canyon heads may constitute a serious obstacle to the turbidity-current hypothesis. Evidence shows that large rivers build out submarine and sublacustrine slopes wherever these streams debouch near such slopes. Accordingly, these areas should be the least likely to have canyons cut by submarine processes. The canyon of the Congo, cut deep into the estuary, is a serious problem, as Woodford has recognized, unless one assumes that the river originally cut this canyon and that after submergence it has been maintained or perhaps recently reopened by a great slide along the old filled gorge.

Submarine Canyons, Gradients and Nickpoints

Woodford is apparently much impressed by the contrast between the longitudinal profiles of the submarine canyons and those of land valleys. He considers that the nickpoints which occur where the canyons approach the shore are proof that the latter were not cut by subaerial erosion. One can certainly agree with him that the simple submergence of a canyon would fail to produce a nickpoint along the valley at the temporary position of the shore line. However, this is an over-simplification of the problem. If the canyons were cut in the remote past and have been submerged over a long period, the nickpoint could be explained by the building of a delta in the drowned estuary out to the present shore line, but leaving the canyon unfilled outside, or by the fill and cut which took place in the submarine canyon following the submergence.

A point which Woodford neglected to mention in his discussion of nickpoints is what happened to the Monterey Canyon as the result of the lowered sea levels of the glacial stages. Unless he believes that the canyon was cut subsea entirely since the last glacial stage, which is most unlikely because of the huge dimensions and the rock walls of the canyon, the lowered sea level should have increased the gradient of the Salinas and caused active cutting into the heads of the pre-existing canyon. This would have given it a subaerial head which, according to Woodford, should have lacked a nickpoint. The subsequent rise in sea level in any case must have redeveloped the nickpoint so that Woodford's submarine origin for the present submarine canyon head from this point of view is no better than the idea of original subaerial excavation.

The discrepancies in gradients between submarine canyons and stream valleys in general, such as those which cut the California coast range, require further consideration. If the coast had been emergent long enough down to the bottom of the continental slope to allow the development of a graded profile and if the submergence had been rapid and recent, one should find the land canyons with gradients continuous with those of the submarine canyons. However, there is no indication that any of these conditions has existed. A relatively short exposure of portions of the continental slope would fail to get the canyons into adjustment with the upper portions. Also the remote submergence would allow the streams in the upper portion to develop a profile completely out of line with that beneath the ocean. Many types of gradient could exist in the canyons now on the sea floor depending on the nature of the rocks, the length of time exposed, and the extent to which the gorges are filled with sediment.

Evidence of Submergence

In the rejection of the hypothesis of subaerial erosion most authors seem to overlook the abundant evidence of large-scale submergence which exists along the borders of continents. If the continental margins have been submerging over a long period of time and if, as is now demonstrated, there is a mechanism for keeping open the ancient river-cut canyons of relatively steep gradient, the chief objection to subaerial erosion seems to have been removed. The present article is not the place to deal completely with the evidence of submergence, but it is easily provided for portions of the east, south, and west coasts of the United States as follows:

(1) The deep Standard Oil borings in Cape Hatteras (Swain, 1947) have revealed terrestrial formations at depths of 6500 feet.

(2) The numerous deep drillings into the Mississippi Delta have yielded shallow-water and terrestrial formations at many thousands of feet depth (Lowman, 1949).

(3) The drillings at the head of Monterey Canyon (Woodford, 1951, p. 835–838) show some thousands of feet of sediments, apparently largely shallow marine or terrestrial in origin.

It does not seem unreasonable that at some time during the past the margins could have been sufficiently emergent to have allowed canyon cutting. Can it be maintained on the one hand that landslides and turbidity currents are incapable of keeping open ancient canyons and on the other than these same processes can produce the canyons independently? Surely it requires much less energy to maintain pre-existent gorges than to excavate new gorge out of solid rock.

Turbidity Currents as Erosive or Transporting Agents

There is no longer any doubt that some agency such as turbidity currents, transports grea quantities of sediment out along the canyo axes and presumably carries the sediment out over the basins beyond the canyon termina tions. The demonstration, of transportin powers does not constitute a demonstratio of erosion. For example, the lower Mississipp River is transporting enormous quantities o sediment into the sea, but it is not erodin its bed in the true sense. It is simply shiftin sediment seaward which was originally erode by headwater streams with higher gradients Similarly, turbidity currents may be merel the transporting agents of material provide by landslides. Ericson, Ewing, and Heeze suggest that erosion is indicated in the Hudso Canyon because of the discovery of chal pebbles, presumably from Eocene beds outcropping up-canyon. Landsliding from the canyon walls, or even on the floor, would accoun for the presence of these pebbles. Similar slide have been discovered in the exploration o California submarine canyons. In fact, it i these slides which appear to be responsible fo the turbidity currents. They stir the sedimen into suspension and thus provide the motiv power.

One looks in vain for evidence that the turbidity currents actually erode. For example they must be set up on steep delta fronts wher slides are not uncommon, and yet these delt fronts are actually being built forward rathe than eroded. Even during the course of slide, deposition can take place directly i front of the slumped material as shown b Woodford (1951, Fig. 8). Nor are these slide on delta fronts producing net erosion since th deposition which follows more than offset any temporary deepening.

The inability of turbidity flows to erode i further suggested by finding cores on stee portions of canyon floors with undisturbed fine-grained deep-water formations overlain by coarse sands (Shepard, 1951a). This indicates that even in the places of high gradients the flows have been incapable of cutting away the soft underlying muds. This finding is entirely in agreement with the reports by Migliorini (Kuenen and Migliorini, 1950) that delicate fossil impressions on the surface of shales underlying the coarse turbidity current deposits are left intact indicating an extremely gentle action of superimposition. The observation of turbidity currents in tanks similarly indicates a suspension moving through the lower portion of a water body without particularly disturbing the underlying surface. The suspension is easily deflected off the bottom and apparently shows no tendency to erode.

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551

DIURNAL FLUCTUATIONS IN BATHYTHERMOGRAMS[1,2]

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Scripps Institution of Oceanography
University of California

ABSTRACT

Series of bathythermograms extending over 12- to 90-day periods from two deep-sea stations in the northeastern Pacific fail to show more than indefinite or minor fluctuations of tidal period, in contrast with marked internal tides which have been observed in the Atlantic. Fluctuations of surface temperature were found to be about half random and half due to diurnal solar heating.

TIDAL PERIODICITY

The ocean stations maintained by the U. S. Coast Guard in the eastern Pacific have made it possible to obtain bathythermograms at frequent intervals over long periods of time. Three sets of such data, extending to a depth of 450 ft. (137 m), well below the thermocline in each case, have been investigated for fluctuations of tidal period. Table I and Fig. 1 describe the data. Spectra were obtained by computation of both periodograms (6) and correlograms (1), the latter with the help of the Marine Physical Laboratory correlator (7). The frequencies examined range from 0.3 cycles/day to the upper limit set by the spacing of the data, either 3 or 12 cycles/day.

In only one of the three cases (Series I) was a statistically significant result found. At 76 m depth, 14% of the total temperature variance (mean squared deviation, a rough measure of the "energy" of fluctuation) represented an approximately diurnal periodicity, the rest being distributed in a continuous spectrum, as shown in Fig. 2. Further numerical results are given in Table II. The other series, II and III, also gave some indications of diurnal or semidiurnal periods, but these were so small as to be of doubtful statistical significance.

TABLE I. Description of Data

Series designation	I	II	III
No. of bathythermograms	390	69	226
Interval between readings, in hours	1	4	4–4–16
Total interval, in days	16	12	91
Dates	19 June to 6 July 1949	12 August to 25 August 1948	1 July to 30 Sept. 1949
Position of stations	30° N, 140° W	30° N, 140° W	49° N, 148° W

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[1] This work represents one of the results of research carried out under contract with the Bureau of Ships, Navy Department.

[2] Contribution No. 551 from the Scripps Institution of Oceanography.

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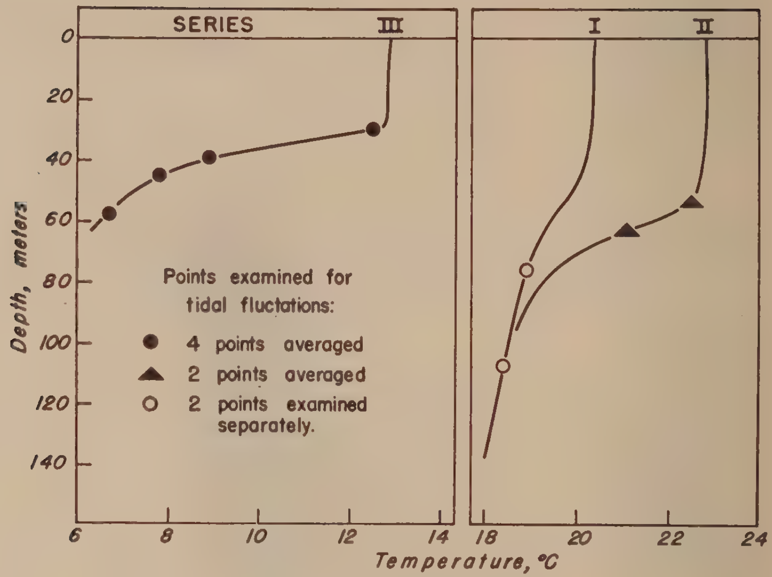

Figure 1. Mean bathythermograms.

In view of the absence of a semidiurnal component in Series I, it should be noted that these observations were taken within two degrees of an amphidromic point located by Harris (5) for the semidiurnal surface tide.

TABLE II. Results of Analysis of Series I

Depth, m	76	107
Total root-mean-square temperature fluctuation, in °C	0.26	0.22
Amplitude of component with 24.5 hour period, in °C	0.12	0.067
Corresponding presumable amplitude of vertical displacement, in m, using mean gradient from Fig. 1	5.4	4.7
Probability that random fluctuation of continuous spectrum (Fig. 2) would give an amplitude as great as that above, for one out of 18 periods investigated	0.003	0.3
Correlation coefficient with temperature at surface	0.09	0.19
Correlation coefficient between temperatures at depths of 76 and 107 m	0.48	

The diurnal component in Series I has been more closely examined for evidence of connection with tides. It was far from constant in magnitude during the 16 days of observations, being most prominent during the final four days, which included a neap-tide epoch. Minimum temperature (and minimum thermocline depth) in this period

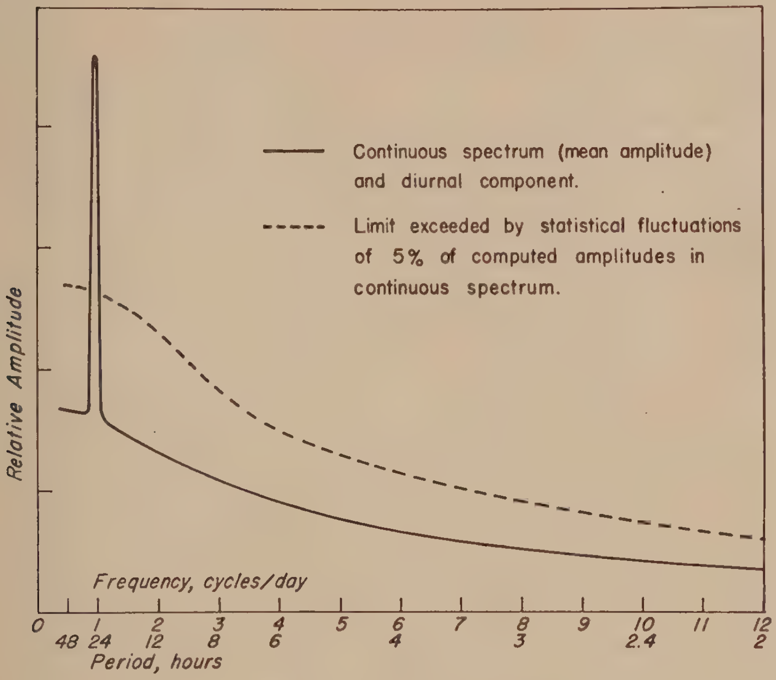

Figure 2. Spectrum for Series I.

occurred three hours later than the upward maximum of the local tide-generating force; the corresponding lag for the diurnal high-water on the surface is five hours in this area. During the remaining 12 days, which included a spring-tide epoch, the component was also traceable with about the same phase, but it was below the level of good statistical significance. Thus, the phase of the internal oscillation corresponds well with that of the surface tide, but the amplitude variation during the fortnight does not. It would seem that the connection with tides is at most a loose one.

Two alternative interpretations have been suggested. Since the observations were made at 30° latitude, where the period of motion in an inertial circle is diurnal, one might suppose that the rather abrupt appearance of distinguishable diurnal oscillations in the final four days of Series I was the result of some impulsive meteorological disturbance whose aftermath could easily involve intertial motion. However, the pertinent weather maps show nothing to support this possibility. Another suggestion is that vertical convection might communicate the influence of diurnal solar heating from the surface to thermocline depth. This seems possible, since the indicated energy of internal wave motion is of the same order as the potential energy which might be developed over a 10-day period by diurnal increase in salinity or by lowering of temperature at the surface.

The most striking aspect of the results is the inconspicuousness of whatever diurnal or semidiurnal periods may exist, in marked contrast with some previous observations. For example, mere inspection of the temperature fluctuation curves of the METEOR anchor station 385 of 1938 (8) at 17° N and 46° W convinces one of prominent semidiurnal oscillations at thermocline depth (80–120 m). Of course, the present data are seriously limited in respect to depth and by the lack of salinity measurements, so that an internal tide at greater depths could have escaped observations. However, deep casts made in the same areas (e. g., CARNEGIE stations 125 at 52° N and 151° W in July 1929 and 146 at 32° N and 141° W in October 1929 [4]) show maximum density gradients at depths of the order of 100 m, which is therefore the region which will generally show the most prominent internal motions. Hence, it does not seem probable that the present data, even though limited to 137 m depth, would completely fail to reveal conditions, if they exist, similar to those found by the METEOR (8, 2) and the ATLANTIS (9, 10) in the Atlantic Ocean.

Defant has expressed the view that internal tides are as widespread as the surface tides (3). Their generation at ocean boundaries seems a very probable process; in contrast, the presence of internal tides in the deep ocean is difficult to understand dynamically. If one narrows the discussion accordingly by considering only deep-sea stations well removed from ocean borders (thus excluding, for example, the SNELLIUS observations in the East Indies) and those occupied for at least two days (for the sake of more conclusive statistics), it then appears that the number of observed cases in this category is not large. Our present result suggests that some limitations exist on the place and manner of occurrence of internal tidal oscillations, which, if established, may in turn contain clues as to their dynamic origin.

SURFACE TEMPERATURES

Unusually good agreement was found between the surface temperature readings from the Series I bathythermograms and the corresponding bucket temperatures. Therefore these have been given some further statistical study. It is assumed that correlation between the two sets of readings arises from true fluctuations of sea-surface temperature and is limited by independent errors in the two methods of observations. This permits separate numerical evaluation of the true RMS (root-mean-square) fluctuations and of the RMS error in each type of observation.

Part of the variance of true temperatures arises from a diurnally periodic component with maximum occurring three hours past local noon; this is presumably due to solar heating. The remaining variance is considered a real random fluctuation, separated from instrumental errors. Table III contains the numerical results.

TABLE III. STATISTICS OF SURFACE TEMPERATURE AND OBSERVATIONAL ERRORS FOR SERIES I

	RMS fluctuation, °C	*Proportion of total variance*
Bathythermogram errors	0.06	
Bucket temperature errors	0.10	
True surface temperature		
total	0.12	100%
random component	0.09	59%
diurnal component (amplitude 0.11 °C)	0.08	41%
Correlation coefficient between bucket and bathythermogram readings	0.68	

Acknowledgment of essential contributions to this study are due the Coast Guard weather-patrol ships and staff members of the Bathythermograph Division and of the Marine Physical Laboratory. Drs. Walter H. Munk and Gifford C. Ewing have contributed valued suggestions on interpretation of the data.

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COMPOSITE ORIGIN OF SUBMARINE CANYONS

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Reprinted for private circulation from
THE JOURNAL OF GEOLOGY
Vol. 60, No. 1, January 1952
PRINTED IN U.S.A.

outward extensions of the subaerially cut submarine canyons.

5. The canyons which remained unfilled were extended headward during a glacial-stage lowering of several hundred feet, and, as a result, Pleistocene material is truncated by the inner branches of the canyons. Furthermore, the canyon heads, having been excavated in relatively recent times, have more tributaries than the older canyons, where many tributaries may have been filled.

6. Slumping has acted on the alluvial and marine deposits at the canyon heads, allowing the formation of shallow valleys in this recent material. In addition, slumping has widened the canyons as it does on land.

The only striking difference between the two hypotheses is that the first assumes that no subaerial excavated canyons existed on the ocean floor in the area where the present canyons are found and hence that they were entirely the product of marine processes; while the second assumes that canyons were cut from time to time in the past and have been maintained and perhaps enlarged

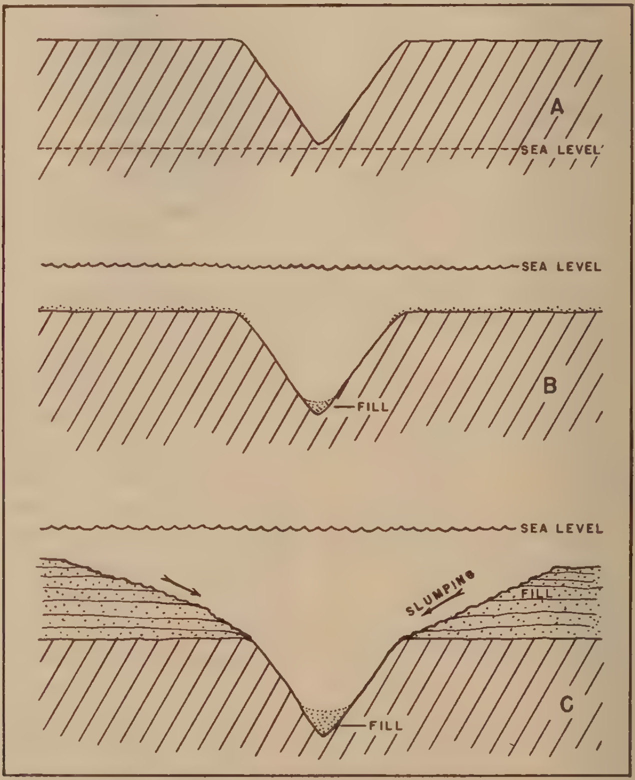

Fig. 1.—Illustration of a sequence which could account for greater canyon-wall height than elevation of continental margin above sea-level. *A* shows a section of the canyon cut into the margin during elevation. *B* indicates the submergence of the margin and initiation of deposition. *C* shows the building-up of the shelf accompanying submergence, while slumping and turbidity currents have prevented excessive fill on the floor of the steeply sloping submarine canyon.

by landslides and density currents. Both hypotheses seem to be dependent on the maintenance of the continental slopes, as it becomes quite obvious that an outbuilding shelf cannot have rock-walled canyons cut into it. If canyons had been cut into the slopes by subaerial erosion at any time during the past, they could, of course, be maintained by any process capable of cutting the canyons. Therefore, the important point to determine is whether or not the continental slopes have been exposed to subaerial processes.

EVIDENCE FOR SUBMERGENCE

Before discussing the possibility that most of the continental slopes of the world and even the slopes of some islands have been considerably submerged, it is important to consider the magnitude of the submergence necessary to account for the canyons. Echo soundings now reveal that submarine valleys can be traced outward to very great depths, even off the supposedly stable east coast of the United States. As indicated previously, however, the outer portions of the valleys may simply represent channels of nondeposition in deeply submerged delta fronts out beyond the lower limits of the subaerially excavated canyons. Therefore, the important point to determine is the depths to which the rock canyons or the deeply incised canyons extend. Unfortunately, we do not now have much evidence as to how deep below sea-level rock-walled canyons do extend. Rock has been dredged in the California canyons from depths of 3,900 feet (Shepard and Emery, 1941, p. 89) and from the Georges Bank canyons at 3,300 feet (Stetson, 1949), and rock was obtained in a core from one east-coast canyon farther south, at a depth of 5,100 feet (Stetson, 1949, p. 33). Survey reports suggest rock bottom in about 3,600 feet in Tokyo Canyon (Shepard, 1948, p. 219). The steep-walled gorges extend down as deep as 6,000 feet in some places, but for the most part the valleys become insignificant at greater depths.

Is it unlikely that portions of the continental slopes have formerly been as much as 6,000 feet above their present level? Support for such a contention is found in the records of well cores on land and from collections on submarine hills outside the coast. A drilling in Cape Hatteras shows the Cretaceous terrestrial formations at a depth of 6,500 feet below present sea-level (Swain, 1947). In Florida and around the Gulf Coast, oil-well drillings show that great submergence has taken place, accompanied by deposition of shallow-water formations. If the continental slope in these areas had persisted, canyons should have been cut during any emergence which alternated with the submergence. Such emergences seem to be indicated by the erosional unconformities of thick sedimentary series.

Off the coast of southern California we find many banks ranging in depths down to about 3,000 feet. These banks yield well-rounded cobbles, as do also the seamounts farther offshore. It is hard to explain the origin of these rounded rocks without shallow-water conditions during the past. Is it not likely that the shelves were also emergent at the time when the banks were at or above sea-level? The recent evidence of great submergence in the coral islands and on the flat-topped *guyots* of the Pacific is in line with the rest of the evidence.

Subsidence must have occurred in extensive areas in the world, and this same widespread subsidence could have brought the eroded portions of the submarine canyons to their great depths. It seems, therefore, rather pointless to attempt an explanation of the cutting of the canyons without the help of the subaerial erosion which could have taken place during the earlier state of emergence.

INDICATIONS FROM DELTAS IN GLACIAL LAKES

One of Daly's principal arguments in favor of the origin of submarine canyons by turbidity currents is the existence of valleys on the fronts of deltas in the Swiss lakes. There is no doubt that such features exist (fig. 2), but they have only moderate depth, about 50–100 feet below surroundings. The gullies are also found on the front of marine deltas, such as the Fraser delta, where it is built into Georgia Strait (see Canadian chart 3429). According to several Swiss investigators (all quoted in Collet, 1925), these gullies are nondepositional features, resulting from deposition on either side like the natural levees of rivers in floodplains. The gullies occur in areas where abundant sediment is being carried down slopes which are, in many places, steeper than the slopes in which submarine canyons are found; and yet these delta slopes do not have canyons cut into them and, so far as we know, are actually prograding. Thus, under highly favorable conditions for underwater erosion, deposition rather than erosion is taking place.[3]

Considering the glacial lakes for further analogy, we find that on the mountainsides above the lakes various canyons have been cut since the end of the glacial period. These are often hundreds of feet deep. If erosion had been taking place on the adjacent steep-sloping lake floors at a rate comparable to that above the lake, there should be similar canyons below the water level. Furthermore, estuaries should be found at the mouths of the land canyons. Actually, there are deltas outside the postglacially carved valleys.

CONTRAST BETWEEN SUBMARINE CANYONS AND DELTA-FRONT DEPRESSIONS

It seems reasonable to suppose that the depressions found in the submarine portions of a delta are the result of combined landslide and turbidity-current action. Figure 1 shows the feature which was found on the steep front of the Rhone Delta in Lake Geneva. It will be seen that this valley has no tributaries, that it has little depth below surroundings, and that it has ridges or "natural levees" next to it. What greater contrast could there be between this valley and the inner rock gorges of Scripps and Tokyo canyons (fig. 3)? On the other hand, the outer end of La Jolla Canyon (fig. 4) is closely similar to the valley of the Rhone Delta.

It is not difficult to imagine the type of valley which would develop on a submarine escarpment, such as a typical continental slope, provided that there had been no subaerial erosion. The sediment on the slopes is capable of sliding, so that landslide scars should form at these places. They should originate at a variety of depths and should be somewhat discontinuous. If sedimentation did not intervene, they might remove all the loose sediment on the slope, down to bare rock. As a result, the sediment on the slope adjacent to the landslide scar would become unstable and tend to slide, moving in part into the neighboring depression. A series of slides might remove all or most of the slope sediment. In this way old rock surfaces could be

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[3] Actual erosion caused by slides does take place at the upper part, leaving a shallow trench of short length and short duration (see Woodford, 1951, fig. 8).

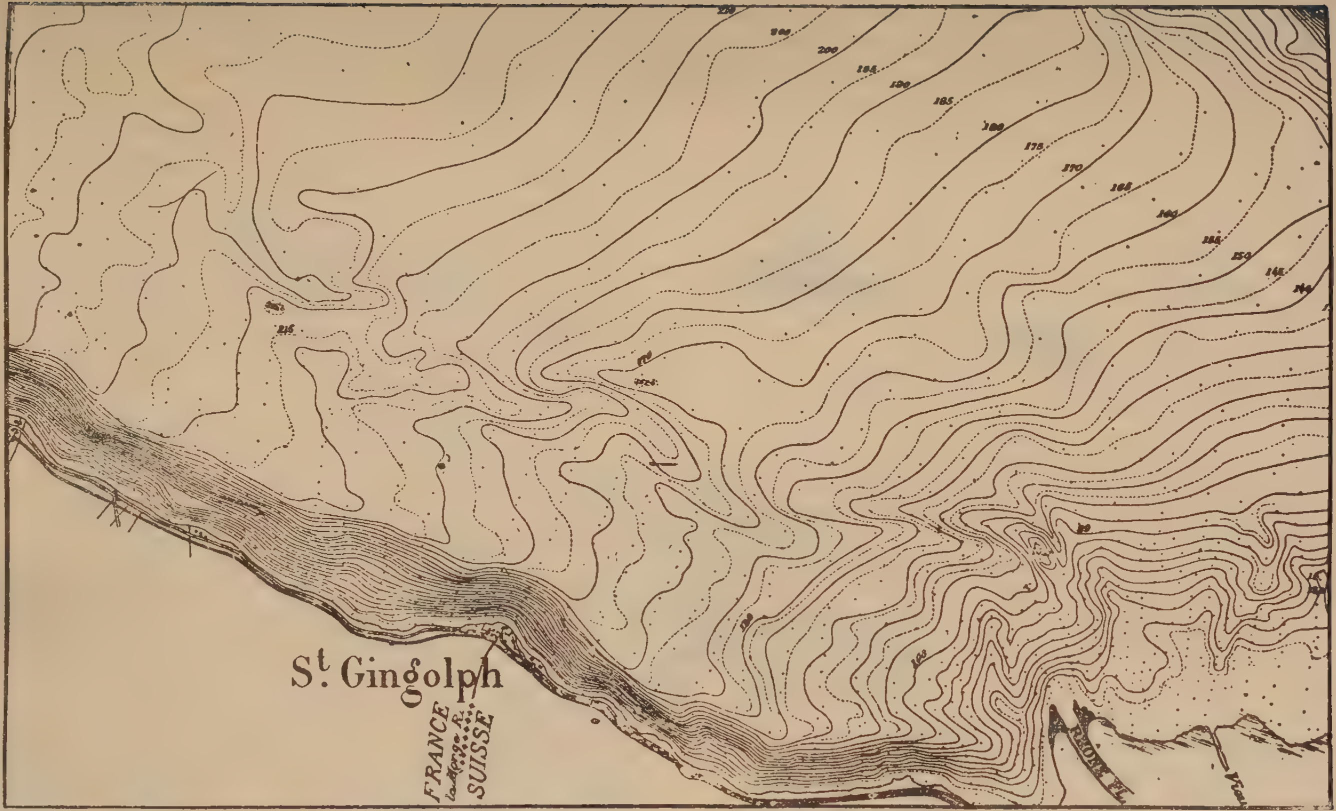
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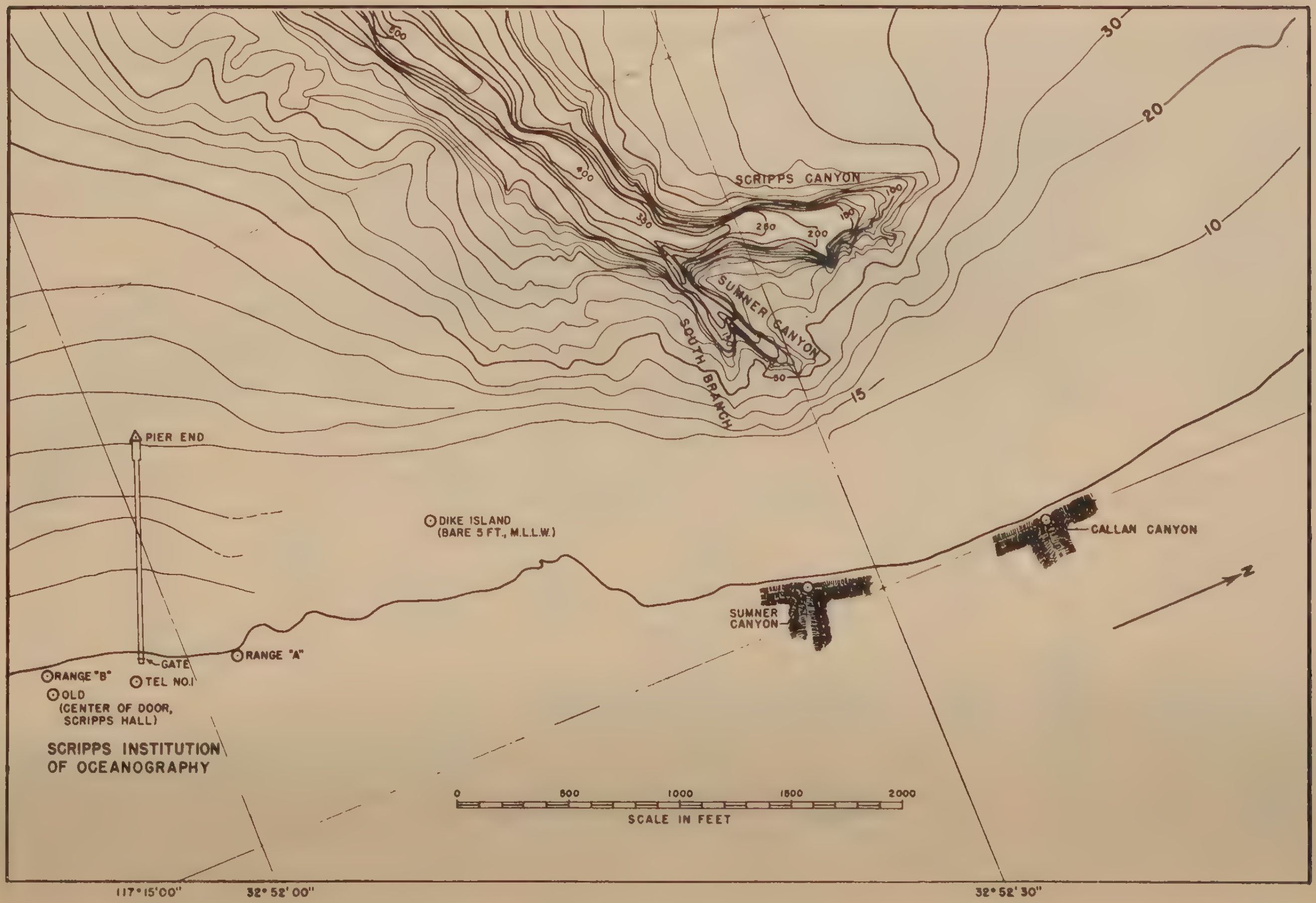
FIG. 2.—Gullies on the front of the Rhone Delta in Lake Geneva. Contour intervals: 5 and 10 meters. From Collet (1925, fig. 42). Compare fig. 4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(BARE 5 FT., M.L.L.W.)
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0
500
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SCALE IN FEET
117°15'00"
32°52'00"
32°52'30"

FIG. 3A.—Scripps Canyon. Contour intervals: 5 feet to 20; 10 feet to 150; 50 feet beyond 150. Comparison with figs. 2 and 4 illustrates the contrast between this rock-walled gorge and the shallow valleys found in the submerged fronts of deltas.

resurrected from time to time, staying uncovered only while sedimentation was negligible; but, in the absence of an appreciable sediment supply, the cutting into the rock surface should be infinitesimally slow, particularly cutting into hard rock, such as the granite of Carmel or Monterey canyons.

LONGSHORE CURRENTS AND CANYON LOCATIONS

Crowell has discussed at length the significance of the supposed location of canyons at points where longshore currents are slowed down, causing deposition of sediments, which he considers would be available for the submarine erosion of the canyons. It is true that the currents are slowed down in the vicinity of canyons as the result of wave-convergence patterns (Shepard, 1950; Shepard and Inman, 1950). This effect, however, is the result of the presence of the canyon, and the retardation actually takes place upcurrent from the canyon head. In bays lacking canyons, the longshore currents

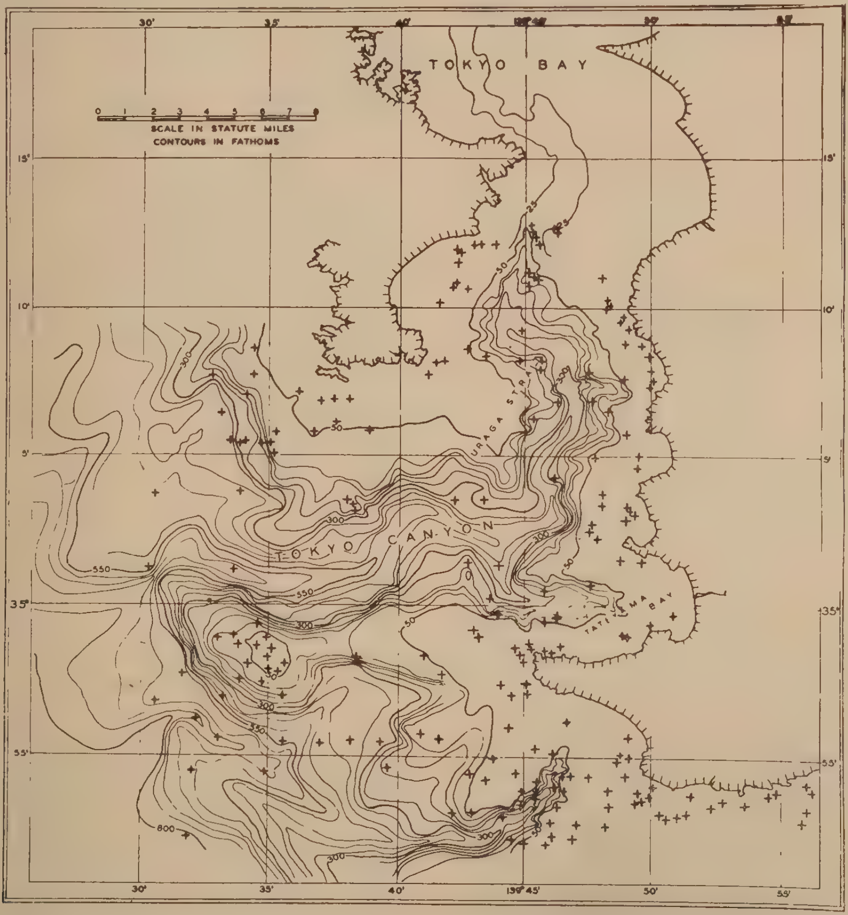


FIG. 3*B*.—Tokyo Canyon. Note that the rock bottom is indicated by crosses. Contour intervals: 50 fathoms, with the 25-fathom contour added in part. Comparison with figs. 2 and 4 illustrates the contrast between this rock-walled gorge and the shallow valleys found in the submerged fronts of deltas.

turn seaward next to points. Because the currents move predominantly from north to south in this region,[4] they are almost invariably deflected seaward at the north side of each projecting point. A careful examination of the California submarine canyon locations shows that there is only one good example of a canyon cut directly north of a point. Several others head within a half-mile of the projecting points, but not where currents normally turn seaward. For example, a northwest blow at La Jolla causes a current along Point La Jolla directly north of the point and well south of the canyon (fig. 5). Crowell recognizes this difficulty so far as Carmel Canyon is concerned but states that the sand necessary to cut this canyon has come around Point Pinos. Actually, the beaches are of such a nature in this area as to indicate that there is no appreciable transfer around these rocky promontories. Extensive beach sampling showed that the main beach at Carmel has sand that is similar to that found in various pocket beaches around Monterey Peninsula, but the sand at the head of Carmel Canyon is strikingly different and has a local origin. The canyons which enter deep estuaries like the Congo (Shepard, 1948, fig. 74) and To-

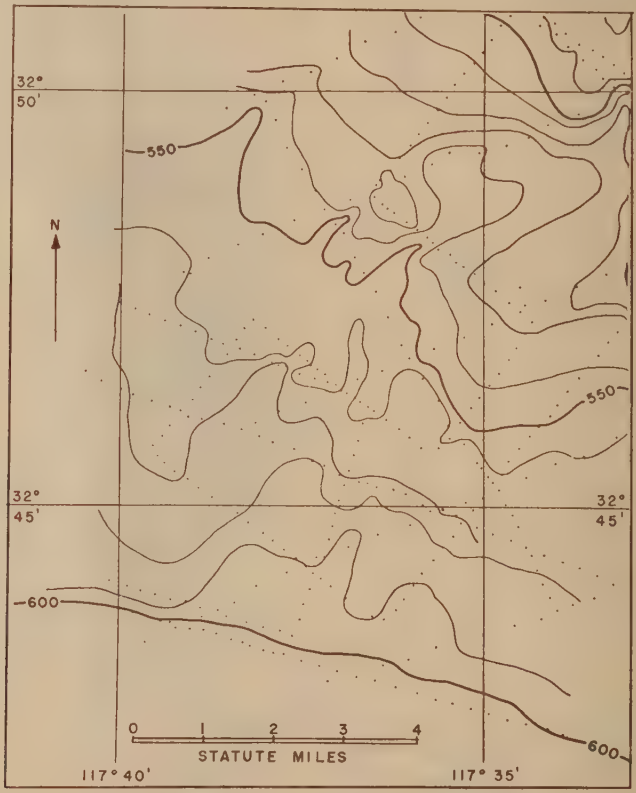


FIG. 4.—The outer portion of La Jolla Canyon. Contour interval: 10 fathoms. Dots indicate positions of soundings. Note resemblance to delta-front valleys and contrast to the inner rock gorges.

[4] Reference is to the California coast.

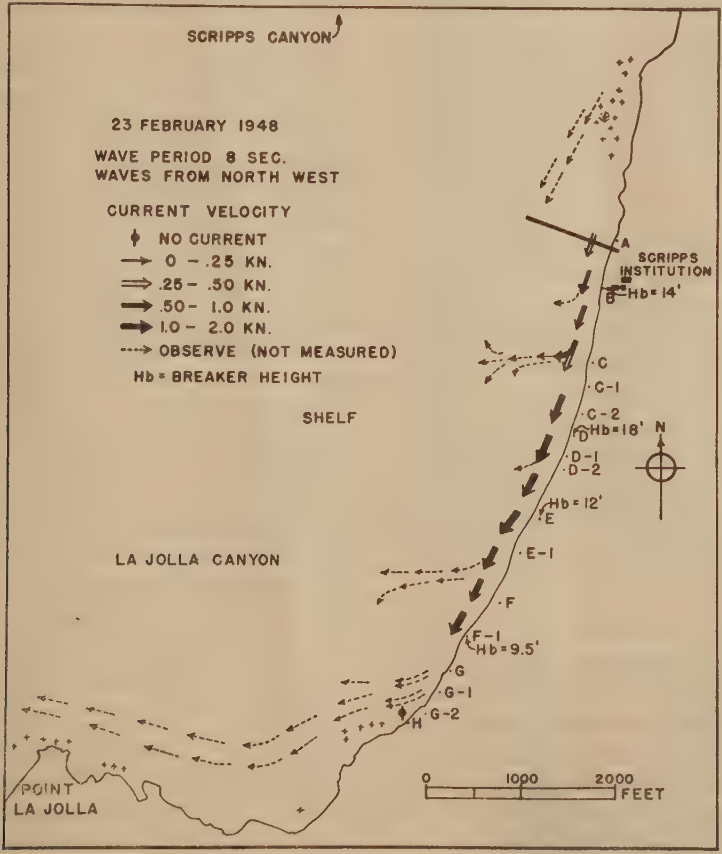
kyo Bay (fig. 3) clearly have no relation to longshore currents.

OBJECTIONS TO SUBAERIAL EROSION OF CANYONS

MAGNITUDE OF EMERGENCE

The most commonly cited objection to subaerial origin of canyons is that it is impossible that all the margins were elevated 10,000 feet in the Pleistocene. No such claim, however, is made, nor is it necessary. Actually, an uplift of about 1,000 feet could account for most of the canyons, provided that the upper portion of the canyon walls consisted of formations laid down after the canyons had been excavated. That is, the shelf margins could have had canyons 1,000 deep cut into them during some early stage and then could have been submerged, followed by the building-up of shelves of younger material and the slumping of portions of this material out along the axes of the canyons (fig. 1).

In view of what we know of the frequent periods of rejuvenation which occur on land surfaces, followed by peneplanation, it would be amazing if during


SCRIPPS CANYON
23 FEBRUARY 1948
WAVE PERIOD 8 SEC.
WAVES FROM NORTH WEST
CURRENT VELOCITY
NO CURRENT
0 – .25 KN.
.25 – .50 KN.
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1.0 – 2.0 KN.
OBSERVE (NOT MEASURED)
Hb = BREAKER HEIGHT
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LA JOLLA CANYON
POINT LA JOLLA
A
SCRIPPS INSTITUTION
B
Hb = 14'
C
C-1
C-2
D
Hb = 18'
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D-1
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FEET

FIG. 5.—Longshore drift accompanying a northwest blow. Note that the principal outpouring of outmoving current hugs Point La Jolla and extends well south of La Jolla Canyon.

the long history of the shelves and continental slopes there had been no episode when moderate uplifts had taken place. On the other hand, some of the submarine canyons, such as Monterey, appear to require rather large-scale emergence of the margins. In view of the well-known instability of the earth's crust, geologists should not be disturbed by such a finding in a few localities.

SCARCITY OF CANYONS

Mention has been made by Crowell of the small number of submarine canyons in contrast to canyons cut into mountain slopes on land. Actually, as soundings increase, submarine canyons are constantly being discovered, so that the contrast in some cases is now very slight. On the other hand, real contrast should not prove disturbing because active sedimentation on the slope should have filled many of the canyons with sediments. Similarly, the small number of tributaries in the outer gorges may be more apparent than real. Submarine trenches, such as Bering Canyon (north of the Aleutians) and Monterey Canyon, have a considerable number of tributaries entering at great depth. No doubt others have been filled. Furthermore, the outermost portions of the marine valleys may lack tributaries because they are of submarine origin like the trenches of the Swiss lakes.

CANYON WALLS OF RECENT ALLUVIUM

Crowell has referred to the evidence that the head of Redondo Canyon is cut into Pleistocene and even Recent formations. Similarly, the formations on the walls of the gullies at the head of La Jolla Canyon (Shepard, 1949, pls. 7–11) are alluvial materials which are very likely not older than Pleistocene and may even be Recent. Crowell considers that these young formations constitute evidence that the canyons must be submarine in origin and still in the process of formation. The point deserves serious consideration.

Turning, first, to the question whether the canyons are still being formed, we are dealing largely with a definition. If the canyons have been cut subaerially and subsequently submerged, leaving steep slopes, there is no reason why the walls should not be subject to slump, or any reason why there should be complete cessation of headward growth, which is caused to a considerable extent by mass movements. Furthermore, the sediment which tends to fill the canyons is also affected by slump, which should leave steep remnants on the sides of the canyon. The same principle is illustrated in figure 1.

The Pleistocene age of the canyon heads is thoroughly understandable because, according to conservative estimates, the sea-level was lowered several hundred feet during the stages of maximum glaciation. This lowering would have allowed streams to flow into the unfilled heads of previously excavated valleys and to have cut the inner gorges, such as those explored in the vicinity of La Jolla (Shepard, 1949). The evidence of these Pleistocene formations, therefore, does not necessarily indicate that the great outer portions of the canyons were cut at such a recent time.

ABSENCE OF LAND VALLEYS INSIDE CANYON HEADS

A number of writers have been impressed with the discovery that there are canyons off portions of the coast where no streams or land valleys exist at the present time. Crowell considers the absence of any evidence that a valley ever existed inside Redondo Canyon as conclusive proof that the submarine canyon was not subaerially eroded. This objection is not so significant as it might seem if one considers other possible sequences of origin. In the first place, one could assume that the subaerially excavated valley never extended landward of this point. Valleys cut on slopes do not extend indefinitely into the plateaus at their heads. In the second place, the canyons may have been excavated before the late Pleistocene and Recent fill were deposited, having been maintained during this deposition by sliding and turbidity currents acting along the canyon axes.

SUMMARY AND CONCLUSIONS

It has been shown that the objections offered to the idea that submarine canyons are the product of subaerial erosion apply only to an abandoned hypothesis that the canyons were cut as the result of huge changes of sea-level during the glacial period. They do not apply to an alternative hypothesis that the canyons were eroded at various times during the past, when the margins happened to be above sea-level, and that they have been maintained subsequently by the sliding-out of the sediment fill and by turbidity currents. It has also been shown that the amount of vertical movement necessary to account for the canyons is not as much as the greatest valley depths indicated in canyon surveys, because the outer valleys are probably due to modification of submerged deltas. The height of walls of canyons is considered now to be a combined product of stream excavation and building-up of sediments on the old surfaces into which the canyons were cut, while slides kept the canyon axes from being filled. The supposed Pleistocene origin of the canyons is now explained as the last of a sequence of events and as the result of exposure of old canyon heads during Pleistocene sea-level lowering which caused headward growth of the old canyons.

The new hypothesis requires supporting evidence of widespread and long-continued subsidence of the continental margins and oceanic islands. Such evidence is becoming available from well records in many areas, including, among others, Cape Hatteras, the outer Mississippi Delta, and various coral atolls. Submergence is also indicated by the numerous finds of rounded cobbles and of shallow-water organisms on the flat-topped banks and seamounts of the Pacific and Atlantic. In view of all this independent evidence, there should be little difficulty in accepting the implication of submergence which has been one of the stumbling blocks in the path of the idea of the subaerial origin of the canyons. On the other hand, the advocates of submarine origin should no longer overlook the implications which are developed by the evidence of submergence.

It is perhaps unfortunate that the advocates of submarine erosion have carried on so little field work in the canyon investigation. The failure to appreciate conditions as they exist in the field is a decided handicap. Thus the suggestion that the California submarine canyons occur on the north side of points, where currents are deflected seaward, is based on deceptively small-scale charts and actually is almost entirely contrary to the facts which we have been gathering (Shepard and Inman, 1950). The steep fronts of deltas built into lakes and fiords appear to offer one of the best testing grounds for evaluating submarine erosion. Presently available evidence suggests that deposition is the dominant process in these places and that any valleys which result are due to localized inhibiting of the deposition either by slides or by turbidity currents. It is to be hoped that someone will investigate both the currents and the depth changes in these ideal localities, so as to see whether turbidity currents really do attain the high velocities which are now claimed for them without any observational basis. It would be a satisfaction to know whether sediments, upon being introduced to slopes of a few degrees, produce erosion or deposition.

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Reprinted from COPEIA, 1951, No. 4

The Locomotor Behavior of Spinal Elasmobranchs with an Analysis of Stinging in *Urobatis*[1]

BERRY CAMPBELL

THE undulatory swimming pattern is as fundamental in the make-up of the members of the phylum Chordata as the possession of a flexible notochord. This swimming behavior is exhibited, in a simple or as a derived pattern, by all forms with the exception of the sessile adult ascidians. The interdependence of these two basic features has been suggested and ably supported by de Lange (1936), whose discussion of the morphology of the chordates emphasizes the relation of the body column and its associated metameric musculature to swimming. According to this interpretation, the segmented effector (muscle) system arranged along the semi-rigid notochord serves the primitive or "Urtyp" locomotion. The phylogeny of the locomotor behavior should be related to the evolutionary history of the skeletal framework, its associated musculature and to the neural integrative apparatus to achieve the full picture of evolution within the phylum.

The nervous structures which integrate this behavior are nowhere more revealingly discussed than in Coghill's (1929) treatise. This author has shown that the appearance of sinuous swimming and of longitudinally conducting motor-cell columns in the spinal cord, in the early *Ambystoma* larva, go hand in hand. This has been amply substantiated by other authors. In the work of Coghill and his collaborators we find a careful tracing of this simple behavior system as it is modified by the developing sensory systems, the growth of limbs, of jaws and gills, and progressive encephalization. Teleosts, amphibians, birds and mammals are all considered. The various papers of this school are discussed and listed in Herrick (1949).

In a previous paper (Campbell, 1940), I have discussed the undulatory swimming behavior of hagfish with intact and transected spinal cords. It was shown that the integrative mechanisms involved were spinal, not cerebral, though the brain influenced quantitatively the locomotor response and integrated it with the environment (righting reflexes, for example). Conditions governing the forward and backward motion of the undulatory waves were explored and the effects of partial section of the spinal cord described. It was shown that immediately upon separation, an isolated portion of the spinal cord acts as a whole, establishing a head and tail end with rather different properties and that the wave length of the undulations adjusts immediately downward as the spinal cord is rendered shorter.

The pelagic sharks, as Gray and Sand (1936) have pointed out, utilize a purely undulatory type of swimming. The resemblance between the progression of these animals and that of the hagfish is striking. Yet certain complications have occurred in the swimming sharks. The development of jaws and of other specialized structures has enlarged the head to a considerable proportion of the entire body length and thus has removed much of the anterior region of the animals from the locomotor apparatus. The body has become relatively shorter and more rigid as compared with the cyclostomes. The development of paired fins has broken the otherwise uniform succession of myomeres and presumably complicated the structure of the spinal cord at the pectoral and pelvic levels. In addition, the assumption of internal fertilization has resulted in the superimposition of a copulatory pattern upon the trunk and tail behavior in both sexes and has led to the fractionation, in the male, of the pelvic fin into locomotor and copulatory parts. Though there are no outward signs of copulatory specialization in the female shark, the spinal cord is the common organ of integration of both swimming and sexual behavior.

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[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 554. The valuable services of Professor Carl L. Hubbs in providing laboratory space and material and, most of all, stimulating advice are gratefully acknowledged. I am indebted to the Scripps Institution of Oceanography for most generous hospitality.

The Batoidei (skates and rays) as well as certain true sharks (Selachoidei) have abandoned the basic simplicity of shark locomotion by utilizing the pectoral fins as propellent organs. This has introduced a radically new behavior pattern. The pectoral fins do not differentiate, in their function, from the trunk in the way that such differentiation is known in the tetrapods. Coghill (1929) has shown the ontogenetic sequence by which the pattern of limb activity from its inception is integrated within the undulatory behavior pattern in the salamander larva. In discussing the relation of stepping behavior to swimming, Gray (1933) and Gray and Sand (1936) have suggested that limb locomotion is a specialization of the basic undulatory pattern. This relationship is obvious in most tetrapods, though exceptions do occur. Within the elasmobranchs, however, a wide range of replacement of the fundamental chordate type of sinuous swimming by a pectoral fin propulsion has occurred. This pattern is peculiar to the group. The phylogenetic sequence in which the present locomotor behavior patterns have been established has recently been questioned by White (1937) in her elaborate and valuable monograph on the phylogeny of the elasmobranch fishes.

The present report concerns the variations in the swimming behavior within the Elasmobranchii. The representative group studied included members of the Selachoidei (sharks) and of the Batoidei (skates and rays), and the following species were represented: *Mustelus californicus* Gill—the gray smoothhound, *Rhinobatos productus* (Ayres)—the shovelnose guitarfish, *Zapteryx exasperata* (Jordan and Gilbert)—the mottled guitarfish, *Urobatis halleri* (Cooper)—the round stingray, *Gymnura marmorata* (Cooper)—the butterfly stingray, and *Holorhinus californicus* (Gill)—the bat stingray. In addition, five 56-mm. embryos of *Mustelus californicus,* delivered prematurely in the aquarium, were available for study.

METHODS

The elasmobranchs utilized in the present study were brought in after capture by seining, trawling, or spearing and placed in a large aquarium tank. Observations on the spontaneous locomotion and on the responses to various stimuli were made on the intact specimens. The animals then were removed and subjected to spinal-cord section immediately behind the head. In some, additional sections were made at more caudal levels. All of the fishes so treated were returned to the aquarium and kept for periods of from 2 to 4 weeks. No difficulty was encountered in maintaining any of the animals except for the exhaustion and multiple abrasion suffered by the *Mustelus californicus.*

Findings

Mustelus californicus (Fig. 1,A) was the only representative of the typical free-swimming sharks used in this study. The locomotor pattern of the intact fish was as described by numerous authors, a simple undulatory progression, not greatly complicated by the fins. Cutting the spinal cord decreased the speed of the wave motion and made automatic the activity which was normally oriented in relation to the physical environment and to the investigator. This was best shown, as previously reported by Gray and Sand (1936), when the spinal fish was supported in midwater in the aquarium. Incessant slow swimming motions were then exhibited. If the spinal preparation was allowed to rest on the bottom of the tank, it frequently showed a weak but perceptible undulation, at other times none. When suspended, so that strong undulatory waves were present, pinching the tail augmented the activity. On the other hand, grasping the forward part of the trunk allowed the observer to inhibit all wave activity. This agrees closely with observa-

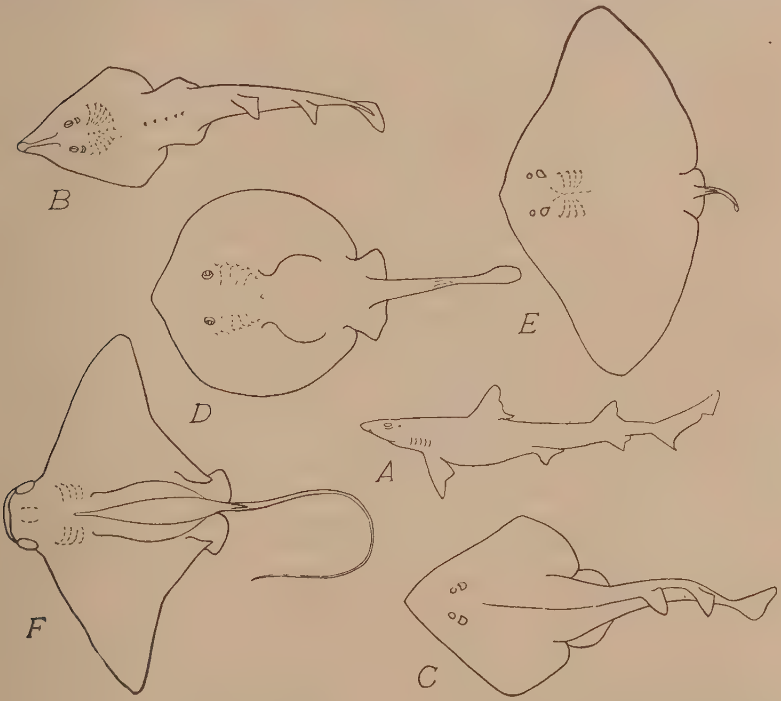


Fig. 1. Sketches showing body form of species studied. A. *Mustelus californicus,* B. *Rhinobatos productus,* C. *Zapteryx exasperata,* D. *Urobatis halleri,* E. *Gymnura marmorata,* F. *Holorhinus californicus.* After Roedel and Ripley (1950), courtesy of California Division of Fish and Game.

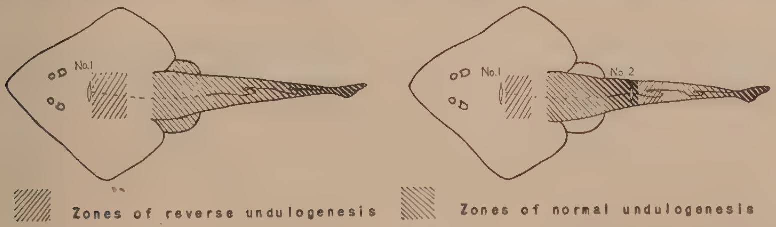
tions, reported previously, on the hagfish, where not only inhibition of normal undulations but the initiation of reverse waves followed stimulation of the gill region. In the adult shark, however, reversing was not induced.

The basic locomotor pattern of this species was lucidly demonstrated in the embryos. A number of different patterns were observed, all of them surprisingly similar to those described by Coghill (1929) in *Ambystoma* larvae. The characteristic activity of the undisturbed embryo (placed in a finger bowl containing sea water) was an incessant swimming type of undulation. Because of the great flexibility of the body, the curves were much more marked than in the adult, but the actual number of waves was the same—a complete sine wave being constantly visible in the active animal. Tactile stimulation of the tail augmented this undulatory activity or, if the embryo were motionless, initiated it. Reversal could be induced by stimulation of the gill region or by tapping the cordlike yolk sac. The reverse waves began at the tip of the tail and progressed along the body axis to the head. Several times it was observed that a reverse wave, unopposed by a contralateral contraction, would cause the entire body to roll up into a circle. This posture tended to be held for some time. The phenomenon is probably to be interpreted as an instance of the stationary waves as described in the hagfish. A variant of this coiling activity, identical with motor activity described in very young salamander larvae, was similar coiling to a full circle which was followed by an immediate snapping back to a straightened position. This was observed several times where coiling was repetitive and to one side, and in one instance where alternate coiling occurred. The motive force for the recovery from the coiled position is obviously the elasticity of the notochord and of the other tissues and not an active posturing. The coils may be looked upon as unopposed unilateral waves of contraction.

The series of species of the Batoidei available for this study showed clearly the transition from the pelagic type of locomotion of the true sharks to one adapted to bottom living (picturesquely dubbed "grovelling" by White). *Rhinobatos productus* (Fig. 1,B), the guitarfish, served for many of the observations. In body form it is exactly intermediate between the sharks and the rays, showing considerable expansion of the head and pectoral fins with no diminution of the trunk and tail. Its swimming pattern shows not only the sinuous undulations of the trunk and tail but also a pectoral fin component quite unrelated to it. In this latter behavior pattern, bilateral waves of extension (dorsal muculature) and flexion (ventral musculature) pass along the borders of the fins. Thus the swimming may still be considered as undulatory, though the nervous integration is entirely of a different sort and is mediated principally by the cranial nerves. The mechanical efficacy of this locomotion is apparent in those fish with their brains and spinal cords severed. Swimming with the pectorals only was rapid and well directed. In the same operated individuals, when the head segment was quiescent, effective locomotion was accomplished with the trunk and tail using the shark-like undulatory pattern. We may conclude, from the independence of these two locomotor patterns in the intermediate elasmobranchs, that the pectoral locomotion is *sui generis* in the Batoidei and that its derivation has not been from the spinally integrated basic swimming pattern. It seems likely that the origin of this behavior is to be looked for in an ancestral gill motor pattern.

Attention in this series of observations was directed mainly toward the undulatory swimming behavior pattern. In the guitarfish, severance of the spinal cord near the head caused little alteration of this behavior other than the environmental dissociation attributable to the loss of labyrinths, eyes, and other sensory organs of the head. The spinal segment showed a caudal predominance of the same nature, but more marked, than that apparent in the spinal hagfish. In the latter form, the head and tail end of the spinal segment each served as sites for the induction of undulation. Stimulation of the head end caused reverse waves, of the tail end normal waves. Quantitatively the two ends varied in threshhold and in the size of the effective reflexogenous area. It took a much lighter stimulus on the tail end to evoke the activity, and the effective area was perhaps ten times as large. In the guitarfish, the same polarity was to be seen. Tactile stimulation on the caudal two-thirds of the spinal segment (including the tail, dorsal and pelvic fins, and the region of the cloaca) caused normal swimming. Only a small area on the dorsum of the trunk had a contrary function. Strong stimulation at this point would inhibit normal undulation but never, in my experiments, induced reversal. (For a special instance, see below in discussion of "stinging" behavior of the rays.) The failure to obtain reversal was not due to an absence of that behavior pattern, for the intact animal when grasped by the rostrum showed vigorous backward swimming.

An important feature of the integrative apparatus of the hagfish was described with the observations on isolated fragments of the body axis. No matter what part of the fish was isolated, the caudal end of the separate portion showed the lowest threshhold to tactile stimulation and the largest area which induced normal undulations. The same phenomenon is to be seen in the elasmobranch as shown in the following experiment on the guitarfish, *Zapteryx exasperata* (Fig. 2). The spinal cord was sectioned close to the head. Later a second section was made across the spinal cord immediately anterior to the first dorsal fin. The area in which this section was placed had, previous to the operation, been within the area evoking normal undulations, though the threshhold was much higher than on the tail. Immediate changes in the behavior evoked by stimulation of the skin in this area were noted after the section. The area innervated by nerves from the tail segment no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▧ Zones of normal undulogenesis

Fig. 2. Illustration of pattern of undulogenic zones in *Zapteryx exasperata* after a single high spinal section, left, and after an additional mid-spinal section, right. The borders of the skin zones fall a short distance behind the second spinal section because of the obliquity of the spinal nerves.

longer served to induce undulation. If swimming of the tail segment were caused by pinching the tail fin, stimulation of the area of the first dorsal fin inhibited this motion. This means that a part of the spinal cord lying in the functional tail end of a large segment had acquired the properties of a head end when a spinal section left it the rostral end of a shorter segment. Related change was to be seen in the integrative meaning of stimulation of the skin innervated by the caudalmost nerves of the trunk segment. This area, which had previously been undulogenic with a high threshhold, became exquisitely sensitive, every slight touch evoking normal undulations in the trunk segment.

So clearly did the elasmobranch spinal cord exhibit the same functional plasticity as that of the hagfish that experiments were performed to test the relation of wave length to length of the spinal segment. In the cyclostome, the wave length became progressively shorter as the cord length was reduced, a phenomenon first observed by Thorner (1932) in similar experiments on snakes. The greater rigidity of the elasmobranchs made observation of the wave pattern of short segments difficult and success in demonstrating the phenomenon was had only with the caudal ends of the fish. In both *Mustelus* and *Rhinobatos* the wave pattern showed progressive shortening as the spinal segment was decreased in length.

The sting ray, *Urobatis halleri* (Fig. 1,D) is, in the series studied, a step more removed from the typical sharks in that the pectoral fins are proportionately larger while the tail and trunk are smaller than in the guitarfish. Intact specimens of this form used the trunk very little in swimming, progression being effected nearly entirely by the bilateral vertical undulations of the pectoral fins, as described above. The principal feature of interest in this species is the specialized trunk behavior which is related to the stinging organ. Though this fish is greatly feared by bathers, in the aquarium it proved very reluctant to sting. Many kinds of noxius stimuli failed to evoke the stinging, but success was finally had by pinning the fish to the bottom of the tank by the sudden application of a large rubber suction disc on the end of a stick. This caused repeated thrusts with the stinging spine. Other stimuli induced only a flight response. Analysis of the reaction pattern became much easier when it was found that a complete release of this performance followed high transection of the spinal cord. In such divided animals, no flight response could be elicited by stimulation of the body posterior to the spinal section. The stinging reaction, however, was revoked by each stimulus to a rather large area of the spinal segment. There was no loss in strength nor in the accuracy of the thrust in the spinal animals as compared with their intact controls, but the ease with which the behavior was evoked was increased by a surprising amount.

The stinging reaction of the spinal animal follows stimulation of the caudal one-third of the pectoral fins, which are innervated by the spinal segment, and by the whole of the surface of the pelvic fins. No response followed the same or greater stimulation of the trunk. The stinging was always directed to the side. That it is a derivative of the reverse undulatory pattern is shown by two types of evidence. A careful visual and cinematic analysis of the action revealed an ipsilateral (to the evoking stimulus) bending of the tail (Fig. 3,A). This starts at the region of the sting and progresses forward.

The sting is thus brought toward the offending stimulus. Then, while the tail is held in a sharp curve, a contralateral contraction high on the trunk draws the stinger back (Fig. 3,B) and an ipsilateral contraction quickly jabs it to a point in space a short distance above the stimulus (Fig. 3,C).

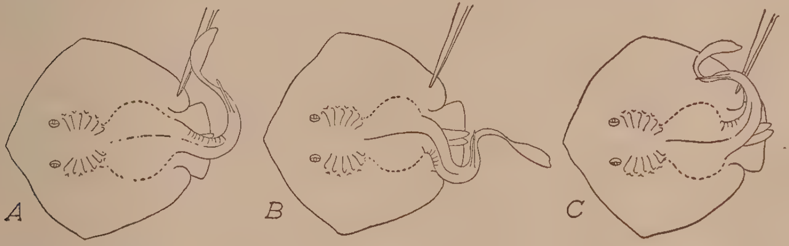

Fig. 3. Sketches from movie of stinging act of *Urobatis halleri*. For explanation of sequence, see text.

The tip end of the tail takes no part in this action. Substantiation of the interpretation of the stinging reaction as reverse undulation is found also in the fact that pinching the tail or otherwise stimulating it completely inhibits the stinging pattern. The tail dominance of the spinal segment inhibits a derived reversing pattern in a way quite in keeping with the observations detailed above and presented earlier in the study of the hagfish.

Two phyletic trends seem to have followed the evolution of the pectoral swimming pattern. One has led to a progressive loss of motility and a strict bottom living habitus. This "grovelling" has been carried to the extreme in *Disceus,* to judge from its morphology, and to a lesser extent in the butterfly sting ray, *Gymnura marmorata,* which was available to me in the living condition (Fig. 1,E). In this species, the trunk and tail are so reduced that the agility with which the stinging spine was handled in *Urobatis* could not be matched and its value as a defensive weapon must be considerably reduced. As in *Urobatis,* marked release of stinging follows spinal section. Undulation of the diminutive body axis could be evoked by pinching the tail and resulted in rapid waving to and fro of that member. When swimming, the intact fish resembles, however, a tailless kite, so insignificant is the caudal appendage.

Another direction of evolution of the Batoidei has led to a re-invasion of the mid-water level. The bat stingray (*Holorhinus californicus*) is the representative of this offshoot which was available in the living state (Fig. 1,F). In it, the trunk and tail are equally reduced in importance as undulatory swimming organs. Far from being a vestigial structure, however, the tail is drawn out into a long filament and seems, upon inspection within the confines of a tank, to have important functions both as a rudder and as a sensory organ.

Discussion

The close interdependence of body form and behavior is borne out by these observations. Though it may appear obvious, I would like to reiterate the contention that in phylogeny the development of behavior patterns proceeds according to the same general laws as does the evolution of structure and, where subject to detailed scrutiny, is fully as reliable an index to relationship as is morphology. In this regard I would like to comment upon the statement in White's monograph to the effect that in elasmobranch evolution grovelling behavior preceded in time and was ancestral to the pelagic swimming. This seems not only unwarranted by the fossil record but least likely from the viewpoint of the student of behavior. Her view is based upon (1) the assumption that in early paleozoic seas, the food supply was limited to the bottom, and (2) that more archaic characters are to be found in the modern representatives of the grovelling forms. On the first line of reasoning, I shall not comment as it seems too hypothetical. The retention of archaic characters, however, does not seem to indicate an unaltered descent from bottom forms, but instead the operation of insular conservatism due to the greatly restricted ecological niches of the grovelling forms. In general, the bottom living forms have restricted ranges in contrast to the frequently world-wide distribution of the pelagic species. Even those members of the Batoidei, such as *Manta,* which have secondarily invaded the mid-water and pelagic zones are inclined to have large ranges. The presence of archaic characters may better be taken to indicate not a continuance of ancestral behavior, but a deviation from it in the direction of a more restricted ecological position. Further support for the view that the pelagic life is primary in elasmobranch evolution stems from the demonstration that the undulatory type of swimming is basic to the chordate phylum. Any view that the Selachoidei are offshoots of bottom living forms is bound to involve unparsimonious postulates concerning the loss, or near loss, of a basic pattern with its subsequent redevelopment.

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